

ECOLOGY OF MOUNTAIN SHEEP:
EFFECTS OF MINING AND PRECIPITATION

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**ECOLOGY OF MOUNTAIN SHEEP:
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A
Thesis

Presented to the Faculty of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

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Fairbanks, Alaska

December 1999

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ABSTRACT

We examined effects of mining on mountain sheep (*Ovis canadensis nelsoni*) in California. Size of home range, forage quality, and diet did not differ between populations in mined and nonmined areas. During summer, we observed the greatest disparity in time spent feeding and diet quality. Because of their dependence on a spring adjacent to the mine, sheep may have spent more time vigilant, and less time feeding. Reducing mining during summer may benefit sheep. We also compared ecology of two female mountain sheep populations from different areas (xeric vs. mesic) in the Mojave Desert. The more xeric Panamint Range was typified by more bare ground, less shrubs, less grass, and larger home ranges than at Old Dad Peak. Females from Old Dad foraged on grasses, whereas those from the Panamints consumed shrubs. We concluded that sheep from the Panamints required larger home ranges because of lower-quantity and quality of forage.

THESIS ACKNOWLEDGMENTS

This thesis is comprised of two chapters, each of which is being submitted for publication to peer-reviewed journals, with myself as senior author. Chapter 1 has been prepared as a manuscript for submission to *The Journal of Wildlife Management*, whereas Chapter 2 is intended for the *Journal of Mammalogy*. "We" in Chapter 1 refers to myself and my co-authors V.C. Bleich, R. T. Bowyer, and M. C. Nicholson, and "we" in Chapter 2 refers to myself and co-authors R. T. Bowyer and V. C. Bleich. This research was supported indirectly by the Institute of Arctic Biology and the Department of Biology and Wildlife at the University of Alaska Fairbanks, California Department of Fish and Game, North Dakota Game and Fish Department, Canyon Resources Corporation, U. S. Bureau of Land Management, U. S. National Park Service, and the San Fernando Valley Chapter of Safari Club International. I am grateful to A. Pauli, T. Swank, B. Pierce, C. Baker, W. Allsup, D. Racine, J. Schlachter, K. Pindel, D. Threlloff, and K. Whitten for field assistance, L. Oehler and M. Oehler, Jr. for preparing forage and fecal sample for lab analyses, S. DeJesus for piloting the helicopter during captures, R. Teagle, B. Nuckolls, B. Gonzales, M. Chechowitz, and others at the California Department of Fish and Game Wildlife Investigations Lab for assistance with captures, and R. Anthes, T. Evans, and E. Forner for flying aerial telemetry. I also thank J. Sedinger, E. Rextad, K. Schwagerle, and R. Barry for statistical advice, J. DeForge at The Bighorn Institute for use of animals housed at that facility, and especially S. Torres for his unprecedented assistance during difficult times, and C. Parrish, K. Mann, and P. McPherson for facilitating our research at

the Briggs Mine. Also, I thank B. Laursen, L. Morisky, J. Romans, and A. Davis for all of their technical assistance. I thank all of my fellow graduate students in the "pit", especially B. Pierce, P. Hessing, C. George, K. Stewart, and M. Keech, for many hours of stimulating discussion, and I am grateful to V. Bleich for his untiring support of this project, and to his wife Teresa for her generosity and support she gave my entire family during this research. Also, many thanks to R. T. Bowyer for his faith in me and his persistence with this project, and to K. Bowyer for her generous hospitality throughout the years. I also am grateful to my parents, Dan and Sonyia, for their patience and support of my many endeavors. Most importantly, I would like to thank my wife Lisa for her unselfish support in ways too numerous to mention, and for enduring more than should ever be expected of a spouse. Finally, I would like to tell my children, Michael Jr. and Rebecca, how much I love them, and thank them for always having a hug and a kiss for me when I returned home from one of my many trips to the field.

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CHAPTER 1.
EFFECTS OF MINING ON THE ECOLOGY AND BEHAVIOR
OF MOUNTAIN SHEEP

ABSTRACT

An understanding of the effects of human activities, including disturbance associated with resource extraction, is essential to the conservation of large mammals. We compared a suite of variables between 2 subpopulations of female mountain sheep (*Ovis canadensis nelsoni*), 1 near an active mine and 1 in a nonmined area, in the Panamint Range, Inyo County, California, USA, to test hypotheses regarding the effects of large-scale mining activities on habitat selection, home-range dynamics, and foraging by this desert ungulate during 1995-97. Size of home ranges, quality of forage, composition of diet, relative abundance of carnivores, and proportions of young to adult females did not differ between mined and nonmined areas. During spring, sheep from the mined area spent more time feeding and had a lower-quality diet ($P < 0.001$) than did females in the nonmined area. Conversely, female sheep from the mined area spent less time feeding during summer ($P < 0.001$) and autumn ($P < 0.001$) than did females in the nonmined area, but continued to have a lower quality diet ($P < 0.001$). Females from both areas were nearest water during summer, whereas in autumn females from the mined area were nearer water than those from the nonmined area. During all seasons, females from both areas selected sites with more mixed-woody scrub habitat, lower elevation, greater slope, and less visibility than did random locations. During summer,

we observed the greatest disparity in time spent feeding and diet quality between female sheep from mined and nonmined areas. During summer, females from the mined area were nearest to the mine, experienced fewer days between blasting, and mining activity (amount of explosives used and ore hauled from the mine pit) was greater than in any other season. We believe that because of their dependence on a source of permanent water adjacent to the mine, female sheep from the mined area may have spent more time vigilant and, concomitantly, less time feeding than conspecifics in the nonmined area. If the patterns we observed persist, reduced nutrient intake could affect reproduction and subsequent recruitment in that subpopulation. We suggest that reducing mining activity during summer may be beneficial to sheep near the mine. Because most females have young at heel during spring, shifting mining activity from summer to spring could be detrimental to those sheep; hence, increasing the interval between blasting during summer may ameliorate the effects of mining on female sheep during that season. Intensity of mining was lowest during autumn. If a shift in mining activity is necessary to offset lost summer production, we suggest autumn for the concomitant increase in activities.

Key words: California, desert bighorn, disturbance, ecology, foraging behavior, habitat selection, home range, mountain sheep, mining, *Ovis canadensis*.

INTRODUCTION

Many researchers (Bleich et al. 1994, Krausman and Etchberger 1995, Van Dyke and Klein 1996, and others) have investigated the effects of human activities on the ecology and behavior of large mammals. Among ungulates, exposure to human activities

has been linked to temporary abandonment of areas of traditional use (Kuck et al. 1985, Bleich et al. 1994), shifts in centers of activity (Van Dyke and Klein 1996), and localized extirpations (DeForge et al. 1981). Quantitative data regarding the effects of mineral extraction on mountain sheep (*Ovis canadensis*), however, are few. Some researchers have investigated the responses of mountain sheep to activities that are likely associated with mining (e.g., helicopter disturbance, Stockwell et al. 1991, Bleich et al. 1994; human disturbance, Hicks and Elder 1979; water development, Krausman and Etchberger 1995). Nonetheless, those authors did not specifically address the issue of mining activities and their effects on the behavior or ecology of mountain sheep.

We studied the effects of a large-scale gold mine on the ecology and behavior of mountain sheep (*O. c. nelsoni*) inhabiting a harsh, desert ecosystem. We measured a suite of variables from 2 demes of female mountain sheep inhabiting distinct geographic areas within a single mountain range (hereafter termed mined and nonmined) to test hypotheses regarding the potential effects of mining on habitat selection, home-range dynamics, and feeding ecology of this unique desert ungulate. Leslie and Douglas (1979) and Krausman et al. (1989) suggested that if preferred habitats and resources are limited or widely dispersed, then size of home ranges of desert sheep should be larger than if preferred habitats and resources were distributed in close proximity to each other. Moreover, Leslie and Douglas (1980) and Krausman and Etchberger (1995) reported that human activity can disrupt normal movements and, thus, influenced the size of home ranges for mountain sheep. We hypothesized there would be no differences in use or selection of

habitat between sheep occupying mined and nonmined areas, and there would be no differences in the size of home ranges between those 2 groups of sheep. We also predicted, that after considering potential resources and predators, female sheep unaffected by mining would select habitat in a manner similar to that of sheep from the nonmined area. Among mountain sheep, vigilant behavior increases in areas with low levels of visibility (Risenhoover and Bailey 1985, Rachlow and Bowyer 1998), and is affected by the presence of a perceived threat (Berger 1978, Stockwell 1991); such behavior reduces time spent feeding, and might result in differences between mined and nonmined areas. Therefore, if sheep near the mine were unaffected by mining, we hypothesized there would be no differences in the proportion of time spent feeding between female sheep from mined and nonmined areas. Moreover, if quality of forage differed between areas, we predicted that individuals consuming lower-quality forage would spend more time feeding to meet their nutrient requirements (Leslie and Douglas 1979). Additionally, if abundance of predators differed between areas, we predicted sheep in areas with more predators would spend more time vigilant (Berger 1978, Rachlow and Bowyer, 1998), and thus spend less time feeding and be less efficient (Molvar and Bowyer 1994).

STUDY AREA

Our study was conducted in the Mojave Desert on the west-facing slope of the Panamint Range, Inyo County, California, about 55 km northeast of Ridgecrest, California, USA (Fig. 1.1). Populations of female sheep near mined and nonmined areas

were centered on Redlands Spring ($36^{\circ}56'37''\text{N}$, $117^{\circ}10'43''\text{W}$) in the south, and Hall Spring ($35^{\circ}57'30''\text{N}$, $117^{\circ}10'55''\text{W}$) about 25 km to the north, respectively (Fig. 1.1).

The Panamint Range is located within the Basin and Range physiographic province, and is characterized by fault-block mountains with a north-south orientation (Norris and Webb 1990). These mountains are composed primarily of metamorphic sedimentary (e.g., sandstones, limestones, conglomerates, etc.) and volcanic assemblages (Norris and Webb 1990). Elevations range from 305 m on the valley floor to 3,370 m at the summit of Telescope Peak. Average annual rainfall from 1911 to 1994 at Greenland Ranch-Furnace Creek was 4.7 cm, and temperature was highly variable, both spatially and temporally; daytime temperatures ranged from 40°C in summer (May-August) to -7°C in spring (January-April), depending on elevation (Death Valley National Park Service Files). Data on weather also were collected at a location adjacent to the study area during 1995-97; during that period, rainfall was sporadic and occurred predominantly during spring (Fig. 1.2). We used historical weather data collected from Greenland Ranch-Furnace Creek, California, and data on the timing of parturition to define seasons for this study. Spring was 1 January-30 April, and was typified by cool temperatures ($\bar{x} = 25$, $\text{SE} = 5.7^{\circ}\text{C}$) and relatively greater precipitation ($\bar{x} = 0.59$, $\text{SE} = 0.99$ cm) than other seasons. Summer was 1 May-31 August; this period was extremely hot ($\bar{x} = 43$, $\text{SE} = 3.8^{\circ}\text{C}$) and experienced little rainfall ($\bar{x} = 0.21$, $\text{SE} = 0.51$ cm). Finally, autumn extended from 1 September to 31 December, and was characterized by cooler temperatures ($\bar{x} = 29$, $\text{SE} = 9.9^{\circ}\text{C}$), and lower precipitation than spring ($\bar{x} = 0.37$, $\text{SE} =$

0.77 cm).

Plant communities in the Panamint Range were described previously by Ginnett and Douglas (1982). Briefly, a creosote bush-scrub (*Larrea tridentata*) community, interspersed with desert washes, occurred on the valley floor and alluvial areas. A shadscale-scrub (*Atriplex confertifolia*) community occupied areas between about 1,460 and 2,320 m elevation, and was dominated by shadscale and blackbrush (*Coleogyne ramosissima*). Above the shadscale-scrub was the sagebrush community with black sagebrush (*Artemisia nova*) and *Chrysothamnus* dominating. Upper elevations (>2,500 m) were characterized by pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*). In moist canyons throughout the study area, mesquite (*Prosopis glandulosa*) was common. Within mined and nonmined areas, there were 8 and 13 permanent springs, respectively.

Death Valley has a full complement of large mammalian carnivores including coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and mountain lions (*Felis concolor*) (Welles and Welles 1961), nevertheless, predation on mountain sheep by those carnivores in Death Valley was thought to be insignificant (Welles and Welles 1961, Weaver 1972). Golden eagles (*Aquila chrysaetos*) also occur in the study area, and prey on mountain sheep (Ober 1931); however, such instances are rare. Other ungulates present in the Panamint Range during our study included feral asses (*Equus asinus*) and mule deer (*Odocoileus hemionus*). Welles and Welles (1961) reported that mule deer were scarce in the Panamints, and was likely the reason that mountain lions also were seldom observed

in that range. In contrast, feral asses have been reported to be abundant in some areas, particularly riparian zones (Ginnet and Douglas 1982).

Most lands within the study area were administered by the U.S. National Park Service or the U.S. Bureau of Land Management and, as a result of the Desert Protection Act in 1994, most roads in those jurisdictions were closed to motorized vehicles. The few roads not included in wilderness areas (e.g., Pleasant, South Park, and Surprise canyons) (Fig. 1.1) were accessible only by 4-wheel drive vehicles, and thus, access was limited. During the cooler portion of autumn and early spring (November-March), open roads were used by 10-15 vehicles per weekend, and 5-10 hikers per week, whereas in summer vehicular traffic and hiking in those areas was nil (M. Oehler, pers. obs., D. Brenner, National Park Service, pers. comm.).

In December 1995, Canyon Resources Corporation began construction of an open-pit gold mine (hereafter termed Briggs Mine) at the mouth of Redlands Canyon (Fig. 1.1); subsequent excavation, crushing, and on-site processing of ore began in March, July, and October 1996, respectively. The Briggs Mine was projected to process ca. 19.3 million metric tons of ore on site during the 7-year life of the mine, and disturb 1,333 ha of land within the 2,350-ha site.

METHODS

Capture Procedures for Sheep

Female mountain sheep were captured during June and October 1995, June 1996, and January 1997, by California Department of Fish and Game personnel using a

helicopter and a hand-held net-gun (Krausman et al. 1985a). All animals captured or observed during those efforts were classified as either adult males or females, or lambs (individuals of either sex, < 1 yr old). Sheep captured in June 1995 were fitted with standard telemetry collars (Telonics, Mesa, Ariz.) and animals captured during subsequent efforts were collared with activity collars (Advanced Telemetry Systems, Isanti, Minn.). Activity collars incorporated a mercury tip-switch oriented parallel to the long axis of the body of the animal that produced different pulse rates, depending on whether the head was up or down. We captured 8 female sheep (5 in 1995 and 3 in 1996) in the mined area, and 11 (8 in 1995 and 3 in 1996) in the nonmined area, and no deaths of animals occurred during any of our capture efforts. During 45 hrs of extensive capture and survey efforts with a helicopter, we observed 22 individual adult females within the mined and nonmined areas, of which 86% were radiocollared during some portion of this study (overall density of 72 female sheep/1,000 km²).

Aerial Telemetry

We attempted to locate all radiocollared mountain sheep weekly during June, July, and August, and in alternate weeks during the remainder of the year using a fixed-wing aircraft (Cessna 185) following the methods of Krausman et al. (1984). Flights for locating collared sheep typically occurred between 0900 and 1400 hr, Pacific Standard Time, and positions of collared sheep were estimated using either LORAN-C or Global Positioning System (GPS) instruments aboard the aircraft. Seventy telemetry flights were flown between June 1995-October 1997; female sheep were located 653 times (340 on

the mined and 313 on the nonmined areas); the number of locations per female ($\bar{x} \pm \text{SE}$) was 48.6 ± 5.8 on the mined and 39.1 ± 3.9 on the nonmined areas. Because of inherent error associated with LORAN-C (Jaeger et al. 1993, Oehler et al. 1996), a correction factor was incorporated (Patric et al. 1988) and was used to adjust data on location obtained with that technology. On average, LORAN-C coordinates indicated the aircraft was 41 m west and 127 m north of the target; all LORAN-C coordinates were corrected by those distances. Because GPS is less subject to geographic variability in accuracy as is LORAN-C (Leptich et al. 1994), we did not correct location data collected while using that technology. Nicholson et al. (1997) estimated that the accuracy of their telemetry locations was 177 m (i.e., circle with radius of 177 m) for their investigation in the San Bernardino Mountains, California. Because we used the same pilot as Nicholson et al. (1997) for most of our telemetry flights, we reasoned that the circular error within our study area would be similar. To be conservative, and because we used > 2 pilots, we increased the radius of the error polygon to 200 m. Krausman et al. (1984) reported similar resolution in accuracy of aerial telemetry, and this level of error has been adopted for other investigations of desert sheep in the Mojave Desert (Longshore and Douglas 1995, Bleich et al. 1997).

Habitat Analyses

Because data on locations of female sheep were used for analyses of both habitat use and home-range size, we first examined those data for departures from assumptions associated with those analyses. Excessive autocorrelation can cause estimates of home

range to be consistently low for using probabilistic models (Swihart and Slade 1985), so we used the multiresponse-sequence procedure (MRSP) of BLOSSOM statistical software (Solow 1989, Slauson et al. 1991) to test locations for each animal for lack of independence. We eliminated data on location until no significant ($P \leq 0.05$) autocorrelation was detected. Consequently, 77 telemetry locations (37 from the mined and 40 from the nonmined areas) were eliminated before performing analyses. The number of independent locations per female sheep ($\bar{x} \pm \text{SE}$) used in subsequent analyses was 43.3 ± 4.4 in the mined and 34.1 ± 3.8 in the nonmined areas.

We pooled telemetry locations of female sheep by area (mined and nonmined) to define areas of habitat available to female sheep in those areas. We used those pooled data sets and the program CALHOME (Kie et al. 1996) to construct a 100% minimum convex polygon around telemetry locations of female sheep from each subpopulation (i.e., mined and nonmined); the resulting polygons were buffered by 1,000 m to account for movements by female sheep which may have been undetected (Bleich et al. 1997). Random locations were generated within each polygon with the same frequency as sheep locations for that area. Next, we used a Geographic Information System (GIS; ARC/INFO, Environmental Systems Research Institute, Redlands, Calif.) to generate a circle with a radius of 200 m around each sheep and random location; habitat within those circles was used to calculate relative use and availability (Nicholson et al. 1997, Andrews et al. 1999). The GIS included a 25-m cell of habitat only if the center of that cell was inside the circle. Thus, a boundary of ± 12.5 m existed around each circle where precise

delineation of habitat was not possible.

A 3-dimensional surface of terrain of the study area was generated from 30-m resolution USGS 7.5' digital elevation models (DEM) with the GRID module of ARC/INFO, and provided information on elevation, slope, and aspect associated with each location. We used the product of the *SD* in slope and the mean angular deviation of aspect (Zar 1984) inside each error polygon as our index to diversity of terrain (Nicholson et al. 1997). Because the resolution of the DEM was 30 m, the radius of the circle used to assess diversity of the terrain was 210 m (i.e., $30 \text{ m} \times 7 \text{ pixels}$). Thus, for elevation, slope, and aspect, a boundary of $\pm 15 \text{ m}$ existed around those circles where precise measurement of those metrics was not possible. To examine the potential role of visibility in determining habitat selection among female sheep, we used the GIS to estimate visibility at each sheep and random location. The GIS calculated the 2-dimensional area (ha) that would be visible from a height of 1 m (approximate shoulder height of a sheep) within a circle having a radius of 1,000 m (i.e., the GIS viewshed).

A map of vegetation communities was developed for the study area with a LANDSAT-TM scene with cells of 25-m resolution. That coverage delineated 6 vegetation communities within the study area, and are cross referenced to descriptions by Ginnet and Douglas (1982), when applicable, follow in parentheses; alkali playa (relatively flat areas on the valley floor), desert-saltbush scrub (adjacent to playas with microphyllous shrubs dominating), creosote-bush scrub, Mojave mixed woody-scrub (shadscale-scrub community), Mojave-woodland scrub (pinyon-juniper woodland), and

bristlecone-pine forest. Because alkali playa, desert-saltbush scrub, and the bristlecone-pine forest represented $< 0.5\%$ of the study areas previously defined, and because female mountain sheep were not located in any of those habitats, those habitats were eliminated from analyses. Additionally, the locations of roads and springs were digitized from USGS 7.5' quadrangle maps for use in home-range analyses.

We used stepwise logistic regression (PROC LOGISTIC; SAS Institute Inc. 1988) with an α -to enter and stay of 0.15 (Agresti 1990) to identify variables (Table 1.1) that might be important in differentiating random locations from those used by sheep. Multicollinearity of explanatory variables was controlled by eliminating one of any pair of variables where the absolute value of $r \geq 0.45$. We determined aptness of the logistic regression model using the Hosmer-Lemeshow test for goodness-of-fit (Agresti 1990). For our habitat analyses, we considered the individual animals as our sampling unit to eliminate potential bias that may be associated with using individual telemetry locations as the sampling unit. Using those variables selected by logistic regression (percent mixed-woody scrub habitat, visibility, percent slope, and elevation), we calculated a vector of means for each female sheep during each season (i.e., 3 vectors for each female sheep). Because availability of habitat does not change by season, we calculated a single vector of means for those habitat variables for random locations in each of the mined and nonmined areas. Finally, we generated a vector of differences for each female sheep during each season (i.e., each sheep vector minus the random vector from its corresponding area); the resulting vectors were dependent variables in a 2-way

multivariate analysis of variance (MANOVA; Johnson and Wichern 1988) to test hypotheses regarding selection of habitat. Main effects in that habitat model were area (mined and nonmined) and season (spring, summer, and autumn), and significance of the model was determined using Wilks' lambda (Johnson and Wichern 1988). Because variables entering our logistic-regression model were important in differentiating locations of sheep from random ones, we considered those variables to be differentially used (i.e., selected or avoided) by female sheep. Selection or avoidance was then determined by subtracting the mean percent availability of a habitat from the mean percent use of that habitat; a positive value implies selection (use > availability), whereas a negative value implies avoidance (use < availability) (Nicholson et al. 1997, Andrews et al. 1999). We used a 2-way ANOVA (random vs. sheep location and season as main effects) to compare distances to the Briggs Mine between sites used by mountain sheep in the mined area and random ones within that area.

Home-range Analyses

Prior to calculating adaptive-kernel home ranges for each sheep, we used CALHOME to estimate the parameter for the optimum smoothing of the 95% adaptive kernel for that sheep (Worton 1989, Kie et al. 1996). Next, we calculated 95% adaptive-kernel home ranges based on 60-120% (in increments of 10) of that smoothing parameter; the value that minimized the least squares cross-validation score for each individual data set was then used as the smoothing parameter for calculating 95, 50, and 10% adaptive-kernel home ranges (Kie et al. 1996). We considered the 10% adaptive-kernel home

range to be the center of activity for a particular sheep; the GIS was then used to measure distances from those centers to permanent springs and roads for our analyses of home ranges.

We used 95% adaptive-kernel home ranges, and plotted home-range area against cumulative sample size to determine whether sample size was adequate. We then estimated the sample size necessary to compute home ranges using the nonlinear procedure in SPSS (SPSS Inc. 1993): home-range size = $A(1 - e^{-bn})$, where A is the asymptote of the equation, e is the base of the natural log, n is the sample size, and b is a constant. Data sets that did not attain 90% of that asymptotic value were eliminated from further analyses (Nicholson et al. 1997). We determined that size of home ranges of sheep attained 90% of the asymptote at sample sizes ($\bar{x} \pm \text{SE}$) of 26.7 ± 2.4 in the mined ($n = 7$) and 26.5 ± 2.6 in the nonmined ($n = 8$) areas. Three individuals lacked an adequate sample and were eliminated from analyses. We tested hypotheses regarding home-range size with data from seasons combined because of inadequate number of locations within seasons.

We analyzed size of home ranges using a 2-sample t -test, and a 1-way analysis of covariance (ANCOVA) with area as the main effect, and distances from the center of activity to nearest spring and road as covariates. We used the multi-response permutation procedure (MRPP) of BLOSSOM statistical software (Slauson et al. 1991) to test our assumption that sheep from mined and nonmined areas were from distinct groups.

Foraging Behavior

Data on head position (i.e., up vs. down) of female sheep fitted with activity collars (mined, $n = 8$; nonmined, $n = 10$) were collected via 2 remote recording stations (Receiver Model 2100, Data Logger Model DCC-5400, Advanced Telemetry Systems, Isanti, Minn.) deployed from March 1996 to September 1997. The telemetry frequency of each sheep was scanned at 15-min intervals until either that frequency was received and a pulse rate could be ascertained, or for a maximum of 1 min. If that frequency was not received within 1 min., the datalogger proceeded to the next frequency in its memory and repeated the previously described process. Each time a frequency was received and a corresponding pulse rate was determined for that frequency, that observation (i.e., an instantaneous scan; Altmann 1974) was coded as either head-up or head-down; the resulting data were then pooled by individual animal at 1-hr intervals. We conducted validation tests for concordance between direct visual observation and the recording system at the Bighorn Institute, Palm Springs, California, USA. One male desert sheep was fitted with an activity collar and the position of its head was recorded every 30 seconds, using the electronic system. Instantaneous-scan sampling (Altmann 1974) was conducted simultaneously with the collection of electronic data to serve as a measure of the "true" activity of the collared animal at that instant; we recorded head position (up or down), and the activity in which the animal was engaged (e.g., feeding, bedded, walking, etc.) at the same time the datalogger recorded its observation. Following the method of Bradshaw et al. (1997), data on head position was used to test the system for accuracy, whereas information on feeding was used to establish a relationship between head

position and time spent feeding. Because we planned to evaluate disturbance associated with the Briggs mine on a daily basis (i.e., days since blasting), we tested our electronic system using that schedule. We used the Z-test for proportions (Remington and Schork 1970) to evaluate the ability of the recording system to correctly quantify the proportion of time an animal spent with its head in a particular position, and to correspondingly compare the proportion of time spent feeding with the position of the head. We further evaluated bias of the recording system (Hansen et al. 1992). The proportion of head-up and head-down observations recorded by the datalogger and the observer ($n = 1,277$) did not differ ($Z = 0.775$, $P = 0.441$); the recording system underestimated head-down positions by 1.2%. Additionally, no significant difference existed in the proportion of time in the head-down position (as indexed by the recorder), or the proportion of time spent feeding (direct observation) ($Z = 0.163$, $P = 0.873$). Bias associated with feeding was minimal with the electronic system (overestimated feeding by 0.2%); consequently, we assumed that a head-down signal indicated a feeding animal (Bradshaw et al. 1997).

Because we knew the days on which blasting occurred at the Briggs mine, we used days since blasting as our measure of disturbance associated with the mine. We used a weighted mixed-model ANOVA (PROC MIXED; SAS Institute Inc. 1997) to test for effects of blasting on the relative proportion of time sheep spent feeding. This model is appropriate when data contain both fixed (e.g., area, season, etc.), and random (i.e., individual animals within the respective areas) components, and exhibit heterogenous variances (SAS Institute Inc. 1997). Proportional data were weighted by the number of

observations that made up that proportion for a female sheep on a particular day and hour. PROC MIXED fitted a mixed-linear model containing fixed and random effects, and allowed data to exhibit correlation and nonconstant variability (SAS Institute Inc. 1997). Fixed effects were area, season, the number of days since blasting occurred (day of the blast, 1-3 days post blasting, and >3 days post blasting), and time period (0100-0459, 0500-0859, 0900-1259, 1300-1259, 1700-2059, and 2100-0059 hr). Interactions involving fixed effects (Table 1.2) were incorporated to help interpret random components (Table 1.3) contained in the overall model. The significance of fixed effects and their interaction was estimated from the Type III estimable functions, with denominator degrees of freedom obtained from a containment method (SAS Institute Inc. 1997). A random component (individual animals nested within area) was incorporated into the model to account for individual variation among animals; interactions incorporating this term also were considered random effects (SAS Institute Inc. 1997), and they included season \times time period \times animals nested within area, and days since blasting \times time period \times animals nested within area. The interaction season \times time period \times animals nested within area was used to test for differences between areas resulting from ecological processes (i.e., seasonal and diurnal patterns), whereas days since blasting \times time period \times animals nested within area was used to test for the effects of blasting (i.e., mining) on feeding ecology of female sheep. PROC MIXED used the method of restricted maximum likelihood to construct the specified linear model, and significance of the random components was computed from the Z-value (the variance

parameter divided by its approximate standard error), which was then tested for a difference from zero (SAS Institute Inc. 1997).

Forage Quality

We collected samples of 12 forage species (5 samples/forage species/area/month) consumed by mountain sheep from July 1995 to June 1996, for analyses of quality following the methods of Bleich et al. (1992). Perennial forb species sampled included desert mallow, desert trumpet (*Eriogonum inflatum*), and Rixford eriogonum (*E. rixfordii*). Perennial grass species included needlegrass, and three-awn (*Aristida glauca*), and representative species of shrubs were bedstraw (*Galium stellatum*), burro-weed (*Ambrosia dumosa*), desert holly (*Atriplex hymenelytra*), brittle-bush (*Encelia farinosa*), Mormon-tea, California buckwheat (*Eriogonum fasciculatum*), and mesquite. After moisture content was determined, samples were ground with a Wiley mill (1 mm screen), and composite samples of each forage species/area/month were created (Bleich et al. 1992) for analyses of percent crude protein ($CP = \% \text{ nitrogen} \times 6.25$), and *in vitro* dry matter digestibility (IVDMD). We measured percent nitrogen with a Leco CNS-2000 Elemental Analyzer (Leco Corporation, St Joseph, Mich.) at the Forest Soils Laboratory, University of Alaska Fairbanks, whereas IVDMD was determined at the Wildlife Habitat Laboratory, Washington State University, Pullman, Washington, with methods described by Tilley and Terry (1963) and using rumen liquor from domestic sheep. We did not quantify the availability of forage in our study areas because of ecological similarities between mined and nonmined areas. We reasoned that the abundance of forage would

not differ substantially, but this potential difference was not addressed.

We analyzed IVDMD and moisture of perennial forbs and shrubs separately using 3-way ANOVA (main effects were area, season, and forage class [perennial forbs and shrubs]). Crude protein of perennial forbs and shrubs was analyzed using a 3-way ranked ANOVA (Conover and Iman 1981) with the same factors as previously described. Because of nonconstant variances when grass was incorporated into the overall model, that forage class was analyzed separately with a 2-way ANOVA (area and season as main effects).

Diet Quality and Composition

Fresh (i.e., < 1 week old) fecal pellets from mountain sheep were collected monthly (June 1995-September 1997) from mined and nonmined areas on approximately the same date each month, and stored appropriately (Jenks et al. 1990) for future analyses. We attempted to collect ≥ 5 pellet groups (25 pellets per group) from each area each month. Fecal samples were ground individually in a Wiley mill (1 mm screen), and percent nitrogen was then determined for each sample as described previously for forage samples. We used fecal crude protein (FCP = nitrogen \times 6.25) as our index to diet quality. Robbins et al. (1987) noted that using FCP as an index to diet quality may be problematic when plant species contain high levels of protein-complexing phenolics; however, several investigators (Leslie and Starkey 1985, Renecker and Hudson 1985, Irwin et al. 1993) have reported a positive correlation between fecal nitrogen and dietary nitrogen for a number of ungulates, including mountain sheep (Seip and Bunnell 1985,

Rachlow and Bowyer 1994, Bleich et al. 1997).

We used composited fecal samples (Bleich et al. 1997) collected between June 1995 and August 1996 to index diet composition. Species composition of fecal samples was determined at the Forage Analysis Laboratory, University of Arizona, with the microhistological technique described by Sparks and Malechek (1968). Three slides per composited sample were prepared (Holechek and Vavra 1981), and the frequency of a species, appearing in each of 20 random microscope fields per slide, was determined (i.e., 60 fields/composited sample). When possible, plant fragments were identified to species. Plant fragments were further categorized into 1 of 4 forage classes (i.e., perennial forbs, perennial grasses, shrubs, or succulents) for statistical analyses (Bleich et al. 1997). Because of potential differential digestibilities among various species of forage (Gill et al. 1983), absolute determination of diets is not possible with this methodology. We assumed, however, that this technique provided an index to the diets of female sheep that could be compared between study areas (Bleich et al. 1997). Diet composition was analyzed using a 2-way MANOVA with forage classes (perennial forbs, grass, shrub, and succulent) as the dependent variable and area and season as main effects, whereas diet quality was evaluated with a 2-way ANOVA with area and season as main effects variables, and FCP as the dependent variable.

Additional Analyses

We indexed the relative abundance of carnivores on the 2 study areas by noting when they were encountered during helicopter flights, and by collecting carnivore feces

while in the field during sampling of plants. Carnivore feces were enumerated and pooled within each area and feces per kilometer of transect for each area was determined and used as a index to the abundance of carnivores for that area (Bleich et al. 1997). We evaluated the relative abundance of carnivores on mined and nonmined areas using a 2-sample *t*-test.

We compared young:adult female ratios between mined and nonmined areas with a binomial approach (Bowyer 1991). We calculated 95% CIs for those estimates and the sample necessary to detect differences in those ratios, recognizing that this methodology is conservative (i.e., overestimates the standard error), and compared ratios between areas for a particular time period with the 95% CIs; where CIs overlapped, we assumed the young:adult female ratio did not differ during that period (Bowyer 1991).

When multi-factor ANOVA was employed, all individual factor levels and their interactions were evaluated; significant models ($P \leq 0.05$) were explored further with the Tukey's honestly significant difference (HSD) test to determine where differences occurred. We analyzed data using the software PC SAS (SAS Institute Inc. 1988 and 1997) and SPSS (Statistical Package for the Social Sciences 1993). We used a Bonferroni correction (Kleinbaum et al. 1988) when conducting multiple comparisons. We examined assumptions of each statistical test and transformed data as necessary to meet these assumptions. Bivariate correlations were evaluated using a Pearson product-moment correlation test (Zar 1984). All values are reported as mean \pm 1 SE unless otherwise indicated, and in all analyses, $\alpha = 0.05$ was adopted for the level of

significance.

RESULTS

Habitat Selection

Logistic regression identified 4 variables (percent of mixed-woody scrub habitat, elevation, percent slope, and percent visibility) that were useful in distinguishing between random sites and those used by female sheep ($X^2 = 4.54$, $P = 0.85$) (Table 1.1). In general, female sheep from both areas selected sites having more mixed-woody scrub habitat, less elevation, greater slope, and less visibility, than did random locations (Fig. 1.3, Table 1.1). When those 4 variables were considered simultaneously in a 2-way MANOVA (area and season), however, no differential selection of those habitat attributes occurred between females from mined and nonmined areas ($F_{8,70} = 0.988$, $P < 0.452$). That is, female sheep from both areas exhibited similar patterns of selection for the same habitat variables throughout the year (Fig. 1.3).

Distance to permanent springs did not enter the logistic-regression model; however, because of an *a priori* hypothesis concerning its importance to desert sheep, we used a 2-way ANOVA (area and season) to address the issue of water availability. When data from both areas were pooled, distance to water was significantly different between random sites and those selected by female sheep ($F_{5,1151} = 4.34$, $P = 0.013$). Further analyses with 2-way ANOVA (sheep vs. random location and area as main effects) by season revealed that after controlling for availability of water, female sheep from the mined area were significantly nearer water than those from the nonmined area during

autumn ($F_{1,364} = 9.27$, $P = 0.002$). During spring and summer, distance to water was not significantly different between areas ($F_{1,232} = 2.69$, $P = 0.102$ and $F_{1,544} = 0.06$, $P = 0.799$, respectively). In general, females from both areas were nearer water than random locations during summer (Table 1.1).

Within the mined area, 2-way ANOVA revealed there were significant differences in the way locations used by sheep and random ones were distributed spatially on the landscape in relation to the Briggs Mine ($F_{5,605} = 19.00$, $P < 0.001$). That outcome was largely the result of sheep being nearer the mine than random locations ($F_{1,605} = 67.09$, $P < 0.001$). Further exploration using 1-way ANOVA indicated there were significant differences between seasons in the distances that sheep occurred from the mine ($F_{2,302} = 6.68$, $P < 0.001$); Tukey's HSD indicated that female sheep from the mined area occurred significantly closer ($\bar{x} \pm \text{SE}$) to the mine during summer ($2,091 \pm 166$ m) than in autumn ($3,267 \pm 340$ m), whereas during the spring sheep were intermediate in distance from the mine ($2,975 \pm 326$ m), and distance from the mine in spring did not differ from that in summer.

Home Range

We used data on locations from 15 female sheep (7 from mined and 8 from the nonmined areas) to compare home range size between areas. Mean size of home ranges did not differ significantly between mined and nonmined areas; home ranges were, however, slightly larger in the nonmined area (Table 1.4). Moreover, sizes of home ranges did not differ between areas after controlling for effects of the distance to the

nearest permanent spring (ANCOVA, $F_{1,12} = 0.482$, $P = 0.501$), or road (ANCOVA, $F_{1,12} = 0.325$, $P = 0.579$).

Foraging Behavior

We collected 10,241 and 7,023 hrs of data on feeding activity for sheep inhabiting the mined and nonmined areas, respectively. Mixed-model analysis of fixed effects revealed that the number of days since blasting had a significant effect on the proportion of time female sheep spent feeding (Table 1.2, Fig. 1.4). Moreover, after controlling for variation among individuals, a significant interaction occurred between area, days since blasting, and time of day (Table 1.3). When a reduced model (all main effects and the interaction days since blasting \times time period \times animals nested within area) was conducted by season, the 3-way interaction was highly significant during all three seasons (Table 1.3). Closer inspection of Z-values indicated the effect was greatest in summer, intermediate during spring, and smallest during autumn (Table 1.3).

Because of the significant outcomes from our by-season mixed-model analyses, we further examined the number of days between blasts using a 2-way MANOVA with days between blasting and amount of explosives per blast as dependent variables, and season as the class variable. Results from MANOVA indicated significant differences between seasons ($F_{4,400} = 3.58$, $P = 0.007$); that outcome was not the result of differences in the amount of explosives used per blast ($\bar{x} \pm \text{SE}$) during spring ($20,462 \pm 1,362$), summer ($23,204 \pm 905$), or autumn ($22,020 \pm 1,280$) ($F_{2,201} = 1.61$, $P = 0.202$), but rather to the number of days between blasts ($F_{2,201} = 5.76$, $P = 0.004$). One-way ANOVA and

Tukey's HSD indicated there were significantly fewer days between blasts ($\bar{x} \pm \text{SE}$) during summer (1.5 ± 0.2) and spring (2.2 ± 0.3) than autumn (3.0 ± 0.4) ($F_{2,203} = 5.76$, $P = 0.004$). There were 3,397,878 metric tons of ore removed from the pit during spring, 4,785,498 in summer, and 2,552,166 during autumn. The amount of ore hauled each month was positively correlated with tons of explosives used during that month ($r^2 = 0.83$, $P < 0.001$).

Forage Quality

We collected 1,152 individual forage samples within the mined ($n = 578$) and nonmined ($n = 574$) areas. A 3-way ANOVA detected no significant effect of area on the moisture content of perennial forbs and shrubs, but differences occurred between seasons ($F_{11,191} = 1.88$, $P = 0.044$), with shrubs having a higher moisture content than did perennial forbs during spring ($F_{3,77} = 3.35$, $P = 0.023$) (Fig. 1.5). Similarly, there were significant differences in IVDMD between perennial forbs and shrubs on a seasonal basis ($F_{11,191} = 3.40$, $P < 0.001$), but no effect of area ($F_{1,191} = 2.90$, $P = 0.090$). Shrubs had consistently higher IVDMD than did perennial forbs during spring ($F_{1,77} = 22.15$, $P < 0.001$) and summer ($F_{1,63} = 6.30$, $P = 0.015$), but this relationship was not as apparent during autumn ($F_{1,49} = 3.30$, $P = 0.075$). Conversely, when an overall model considered crude protein of perennial forbs and shrubs, there were no area or seasonal effects ($F_{11,191} = 0.90$, $P = 0.546$).

When perennial grasses were analyzed separately with a 2-way ANOVA (area and season), there were significant seasonal differences occurred in the amount of crude

protein in perennial grasses ($F_{5,23} = 7.52, P < 0.001$); further examination using 1-way ANOVA and Tukey's HSD revealed that those differences were because of perennial grasses in both the mined ($F_{2,11} = 6.55, P = 0.017$) and nonmined ($F_{2,11} = 9.87, P = 0.005$) areas having higher protein content during spring. Likewise, 2-way ANOVA (area and season) models indicated significant differences in IVDMD ($F_{5,23} = 6.42, P < 0.001$) and moisture content ($F_{5,23} = 4.52, P = 0.008$) of perennial grasses from mined and nonmined areas. Again, those differences were driven largely by the effects of spring conditions; IVDMD was significantly higher ($F_{1,5} = 29.58, P = 0.005$) on the mined than the nonmined area ($\bar{x} = 66.4 \pm 4.7$ and $\bar{x} = 42.5 \pm 5.9\%$, respectively) during spring. Moisture content of perennial grasses did not differ between areas ($F_{2,23} = 2.18, P = 0.157$), but was significantly higher during spring than autumn ($F_{2,11} = 7.39, P = 0.013$). Overall, there was a clear trend in increasing quality of forage among all classes during spring (Fig. 1.5).

Diet Quality and Composition

We collected 175 individual pellet groups from mined and 184 from the nonmined areas for assessing quality of diet of sheep. A 2-way ANOVA indicated there were significant area and season effects on the quality of diets ($F_{13,358} = 32.18, P < 0.001$) (Fig. 1.6). One-way ANOVA (area as main effect), conducted by season, further revealed those differences were the result of female sheep on the nonmined area having consistently higher levels of FCP than conspecifics in the mined area. Moreover, diet quality peaked during spring (Fig. 1.6), which was consistent with forage classes having

higher levels of crude protein, moisture, and increased digestibility during spring (Fig. 1.5). Although the level of tannins in shrubs may have increased FCP, this is unlikely because there was no association between FCP and the amount of shrubs in the diets of sheep from mined ($r^2 = 0.882$, $P = 0.118$), or nonmined ($r^2 = -0.268$, $P = 0.732$) areas.

Two-way MANOVA, with area and season as factor levels, indicated significant differences between mined and nonmined areas in the proportions of the various forage classes in the diets of female sheep ($F_{8,32} = 1.27$, $P = 0.292$). During all seasons, shrubs were the most prevalent component in diets of sheep from both areas (Table 1.5). Overall, diets of female sheep from the Panamint Range averaged 55% shrubs, 30% forbs, 11% succulents, and 4% grasses.

Other Analyses

There were 7 mortalities of collared female sheep in the nonmined and 2 in the mined areas. In the nonmined area, 2 mortalities were attributed to predation by mountain lions, 1 fell to its death, and the causes of death for the other 4 could not be ascertained. Additionally, the causes of mortality for 2 female sheep in the mined area could not be determined. No differences existed in the proportion of young to adult females between mined and nonmined areas (Table 1.6).

From July 1995 to September 1997, 24 and 34 km of transects were sampled for carnivore feces from the mined and nonmined areas, respectively. When those feces were pooled by area (mined, $n = 32$; nonmined, $n = 36$), there was no significant difference in the number of feces per km between these areas ($t_{22} = -1.91$, $P = 0.077$). During the

course of fieldwork, no carnivores were sighted on the study area; however, most of that work was performed during the day. Additionally, no sightings of carnivores occurred while conducting captures of sheep (45 hr of helicopter flight-time).

DISCUSSION

Overall, differences in the ecology of female desert sheep inhabiting mined and nonmined areas were not large. For instance, the proportion of young to adult females was not different between mined and nonmined areas (Table 1.6). That result indicated that young did not experience differential mortality between those areas; however, samples sizes were small (Table 1.6). Moisture content, crude protein, and IVDMD of all forage classes were highest for both areas in spring, intermediate in summer, and lowest during autumn (Fig. 1.5). Those outcomes are consistent with patterns in the quality of forage observed for other desert ranges inhabited by mountain sheep (Krausman et al. 1989, Bleich et al. 1997). With one exception, we did not detect significant differences in the quality of forage between our study areas; IVDMD of grass was higher in the mined area during spring (Fig. 1.5). We detected no differences in composition of diets between female sheep from mined and nonmined areas, although clear differences existed within each area in proportions of forage classes consumed in different seasons (Table 1.5). The former outcome is probably the result of the similarity in quality (Fig. 1.5) and presumable availability of forage between sites, while the latter outcome is likely a consequence of how desert plants with different life-histories respond to variation in precipitation (Beatley 1974) (i.e., female sheep utilized forage classes differentially,

depending on seasonal quality and availability).

We failed to reject our null hypothesis that size of home ranges for female sheep in mined and nonmined areas would not differ (Table 1.4). Although mean size of home ranges were slightly larger in the nonmined area, there was a great deal of individual variation and no clear pattern to those data (Table 1.4). Berger (1991) suggested that use of steep rocky habitats was more pronounced for post-parturient female mountain sheep compared to those without young. In contrast, females without offspring were more likely to forage in areas away from escape terrain, where quality of forage was better, but perceived risk of predation higher (Berger 1991); those factors likely could result in larger home ranges for females without young. Thus, variability in sizes of home range in our study may have been an outcome of not all collared females having young at heel. Because we were unable to ascertain the reproductive status of every female when data on location were collected (i.e., during aerial telemetry), potential size differences of home ranges for females with and without young cannot be addressed.

We also failed to reject our null hypothesis that habitat use would be similar between female sheep from mined and nonmined areas. During all seasons, females from both areas selected sites having more mixed-woody scrub habitat, lower elevation, greater slope, and less visibility, than did random locations (Fig. 1.3, Table 1.1). Several researchers (e.g., Berger 1991, Bleich et al. 1997, and others) have reported that female sheep consistently used steep and rugged terrain that was close to water. That strategy likely represents a tradeoff between decreased forage quality in steep rocky habitats and

decreased rates of predation on neonates (Berger 1991, Bleich et al. 1997, Rachlow and Bowyer 1998). In addition to the mixed-woody scrub habitat, the other major habitat present in our study areas was the creosote-bush scrub community (Table 1.1). Although creosote-bush scrub did not enter our logistic regression model, observations made during aerial telemetry and capture efforts indicated that this community received most use by female sheep during spring. Following precipitation in early spring (Fig. 1.2), the proportion of grasses increased in the diets of sheep from the nonmined area (1.8 % in autumn to 4.1% in spring), but not for those in the mined area (1.5 % of diet in autumn and 1.1% in spring) (Table 1.5). That difference was not significant; however, that females in the nonmined area increased their use of that resource is consistent with other studies that noted an increase in the consumption of graminoids by mountain sheep following periods of precipitation (Wehausen and Hansen 1988, Berger 1991). Berger (1991) suggested that pre-parturient females that foraged at low elevations on open slopes, made a tradeoff between an increased risk of predation for the opportunity to maximize nutrient intake. Females from the nonmined area had higher levels of FCP during spring than did those from the mined area (Fig. 1.6); such an outcome would be consistent with the strategy suggested by Berger (1991). We hypothesize that females from the mined area may have been reluctant to forage on low-elevation slopes during spring because of the proximity of those sites to human activities associated with Briggs Mine.

We rejected our null hypothesis that patterns of feeding would be similar between

these groups of female sheep (Fig 1.4, Table 1.3). Interpretation of results on feeding ecology during spring, however, is not straightforward. Much of the variation associated with time of day was a result of variation among individuals (Table 1.3). If females in the mined area were precluded from foraging on graminoids during spring, they may have foraged more intensively (i.e., more selectively) in steep areas where forage quality is lower (Bleich et al. 1997). Indeed, quality of diet was lower for female sheep in the mined area during that period (Fig. 1.6). Although bighorn sheep may habituate to human-caused disturbances (Morgantini and Worbets 1988), these ungulates have been reported to avoid areas where disturbance was elevated (Leslie and Douglas 1980, Berger 1991, Stockwell et al. 1991), and do not habituate to extreme disturbance such as helicopter overflights (Bleich et al. 1994).

The availability and juxtaposition of water within each area may be the most parsimonious explanation for differences we observed in feeding ecology between these groups of females during summer. Indeed, female sheep from both areas were nearer water during summer than other seasons (Fig. 1.3, Table 1.1). Permanent sources of water were fewer and more dispersed in the mined area (Fig. 1.1). As a consequence, female sheep in that area relied almost exclusively on Redlands Spring to meet their metabolic needs for water during summer. In contrast, females in the nonmined area had access to several springs (Fig. 1.1). Turner (1973) suggested that daily needs for water for desert bighorn sheep were about 4% of their body weight, and that this amount could not be obtained from forage during the hot summer (but, see Krausman et al. 1985b).

Alderman et al. (1986) reported that in the Little Harquahalas Mountains, Arizona, where permanent water was not available, desert sheep likely used pools of free-standing water that accumulated in depressions in the substrate after occasional thunderstorms to meet their metabolic needs for water. During our investigation, however, summer thundershowers were extremely rare (Fig. 1.2); the lack of summer rain and the subsequent formation of dispersed sources of free water, likely would have limited the areas that could be used by desert sheep during that season. As a consequence of reliance of sheep on primarily 1 water source (Redlands Spring) during summer, sheep in the mined area also were closest to the Briggs mine during that season (Fig. 1.1, Table 1.1). Several studies have reported that the magnitude of a response to a disturbance is a function of the proximity to the stimulus (MacArthur et al. 1982, Stockwell et al. 1991, Bleich et al. 1994). Stockwell et al. (1991) concluded that mountain sheep in the Grand Canyon, Arizona, foraged more efficiently as distance from helicopter disturbance increased. Similarly, MacArthur et al. (1982) reported mountain sheep in Alberta, Canada, exposed to low-flying aircraft (90-250 m), exhibited a 3.5 fold increase in heart rate over those exposed to high-flying aircraft (>400 m). Results from our analyses of feeding ecology and diet quality indicate that female sheep in the mined area may have been disturbed by activities associated with the Briggs Mine during summer. That outcome is consistent with the interval between blasting ($\bar{x} \pm \text{SE}$) being shortest during summer (1.5 ± 0.2 days). Moreover, amount of ore hauled from the mine pit also was highest during summer, and was strongly correlated with the amount of explosives used

at the mine. Patterns of decreased feeding by sheep in the mined area (Fig. 1.4) may have been the result of those females spending more time vigilant, and concomitantly less time feeding (Berger 1991, Stockwell et al. 1991). That conclusion also would be consistent with sheep in the mined area having a lower quality diet during summer than sheep from the nonmined area (Fig. 1.6) as a consequence of decreased foraging efficiency (Berger 1991, Stockwell et al. 1991, Molvar and Bowyer 1994). Summer was the season when the greatest disparity in quality of the diet occurred between these groups of female sheep (Fig. 1.6).

Differences in levels of feeding during autumn were similar to those of summer for sheep in the mined area (i.e., consistently lower than the nonmined area) (Fig. 1.4). Interpretation of differences in autumn, however, is less clear than for summer. During autumn, levels of feeding were most similar between those groups of females (Fig. 1.4, Table 1.3). Increased similarity between areas may have been an outcome of sheep from the mined area moving away from Redlands Spring (Table 1.1), and consequently Briggs Mine as well, as daytime temperatures decreased, and reliance on a near water source lessened (Turner 1973). Moreover, an increased interval between blasting at the mine, and subsequently less ore removed during autumn than summer may have ameliorated disturbance to mountain sheep. Quality of forage was lowest during autumn (Fig. 1.5); however, decreased water requirements associated (Turner 1973) with lower temperatures (Fig. 1.2), probably allowed sheep in the mined area to venture away from Redlands Spring in search of higher-quality forage. We hypothesize that the resultant increase in

feeding by sheep in the mined area during autumn (Fig. 1.4), and the least difference in quality of diet between areas (Fig. 1.6), may be the result of those animals moving further away from the area of disturbance (Stockwell 1991) as the physiological demands for water became less severe (Turner 1973).

A combination of 4 factors may offer the best explanation for our results in this study: 1) philopatric behavior of female mountain sheep (Geist 1968); 2) limited number of permanent sources of water in the mined area; 3) close proximity of the Briggs Mine to a primary source of water used by females in the mined area; and 4) lack of rainfall during summer and autumn. In concert, those factors likely resulted in female sheep remaining near the mine where disturbance was greatest, particularly during summer when metabolic needs for water also were highest (Turner 1973). Leslie and Douglas (1980) reported that female mountain sheep in Nevada altered their watering patterns in response to construction activities near a primary source of water. In contrast, we did not observe such a result in our study, presumably because of the high degree of fidelity of female sheep to Redlands Spring, and the lack of other familiar sources of water. If the outcomes we observed persist for sheep in the mined area, it is possible that reduced nutrient intake could result in changes in the demographics of that subpopulation.

MANAGEMENT IMPLICATIONS

Because observed differences were most pronounced during summer, we suggest that reducing mining activities during that period may be beneficial to sheep occupying areas near the mine. Because most females have young at heel during spring, we believe

that shifting mining activity from summer to spring could be detrimental to those sheep. Increasing the interval between blasting, which would subsequently result in a decrease in overall mining activity during summer, may ameliorate the effects of mining during that season. Intensity of mining, as indexed by days between blasting, amount of explosives used, and amount of ore hauled from the pit, was lowest during autumn. If a shift in mining activity is necessary to offset lost summer mine production, we suggest that autumn is the best time for the concomitant increase in activities.

ACKNOWLEDGMENTS

This study was supported indirectly by the Institute of Arctic Biology and the Department of Biology and Wildlife at the University of Alaska Fairbanks, California Department of Fish and Game, North Dakota Game and Fish Department, Canyon Resources Corporation, U. S. Bureau of Land Management, U. S. National Park Service, and the San Fernando Valley Chapter of Safari Club International. We thank A. Pauli, T. Swank, C. Baker, W. Allsup, D. Racine, J. Schlachter, K. Pindel, D. Threlloff, and K. Whitten for field assistance, L. Oehler and M. Oehler, Jr. for assistance with forage samples, S. DeJesus for piloting the helicopter during captures, R. Teagle, B. Nuckolls, B. Gonzales, M. Chechowitz and others at the California Department of Fish and Game Wildlife Investigations Lab for assistance with captures, and R. Anthes, T. Evans, and E. Forner for flying aerial telemetry. We are grateful to J. Sedinger, E. Rextad, K. Schwagerle, and R. Barry for statistical advice, J. DeForge at The Bighorn Institute for use of animals housed at that facility, and especially S. Torres for his assistance during

difficult times. We also thank C. Parrish, K. Mann, and P. McPherson for facilitating our research at the Briggs Mine. All aspects of animal handling complied with protocols set forth in the California Department of Fish and Game animal restraint handbook (Jessup et al. 1986), and were consistent with methods adopted by the American Society of Mammalogists (Committee on Acceptable Field Methods, 1998). This is a contribution from the California Department of Fish and Game Mountain Sheep Conservation Program and is Professional Paper 016 from the Eastern Sierra Center for Applied Population Ecology.

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Table 1.1. Habitat characteristics of random locations and of female mountain sheep from mined and nonmined areas in the Panamint Range, Inyo County, California, USA, (1995-97).

Habitat variables	Area													
	Random		Mined						Nonmined					
			Spring		Summer		Autumn		Spring		Summer		Autumn	
	(n = 576)		(n = 65)		(n = 150)		(n = 88)		(n = 53)		(n = 124)		(n = 96)	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Distance to springs (m)	1,925	40	2,060	118	1,608	83	1,922	97	2,113	133	1,724	84	2,238	89
Distance to roads (m)	1,846	50	1,501	112	1,579	56	1,814	83	1,508	133	1,726	89	1,363	93
Distance to Briggs (m)	12,059	367	2,975	326	2,091	167	3,267	340	19,698	651	21,092	320	20,960	436
Sin aspect ^a	-0.43	0.02	-0.52	0.03	-0.47	0.02	-0.43	0.04	-0.48	0.04	-0.40	0.03	-0.45	0.03
Cos aspect ^b	-0.07	0.02	-0.04	0.04	-0.08	0.04	-0.07	0.05	-0.13	0.06	-0.21	0.04	-0.10	0.05
Slope (%) ^c	26.1	0.3	27.5	0.8	30.5	0.5	28.6	0.6	27.1	0.7	29.9	0.6	26.7	0.7
Terrain index ^d	526	12	664	31	545	21	573	30	575	39	498	20	534	29
Elevation (m) ^e	1,324	25	1,128	39	1,164	26	1,256	27	1,112	40	1,250	27	1,157	37
Visibility (ha) ^{e,e}	0.61	0.02	47.0	3.4	51.4	2.0	45.9	2.8	49.7	3.8	59.6	2.6	55.1	3.1
Creosote-bush	7.3	1.0	3.7	2.2	0.9	0.7	0.0	0.0	3.9	2.4	0.9	0.6	2.9	1.6

Juniper-woodland	11.6	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.8	1.0	1.0
Mixed-woody scrub ^c	79.56	1.6	95.5	2.6	99.1	0.7	100	0.0	96.1	2.4	98.4	1.0	96.0	1.9

^aN-S aspects.

^bE-W aspects.

^cVariables selected by logistic regression model for differentiating random locations from those used by female sheep.

^dSD slope times angular deviation of aspect (Nicholson et al. 1997).

^eViewshed analysis from ARC/INFO; area (ha) visible to a sheep (1 m in height) to a maximum distance of 1000 m based on topographic relief.

Table 1.2. Significance of fixed effects from mixed-model ANOVA (SAS Institute Inc. 1997) on activity of female mountain sheep from mined and nonmined areas in the Panamint Range, Inyo County, California, USA, (1995-97).

Source ^a	NDF ^b	DDF ^c	<i>F</i> ^d	<i>P</i>
Area	1	227	2.50	0.115
Season	2	227	0.49	0.616
Days since blasting	4	334	17.68	< 0.001
Time period	5	227	1.02	0.408
Area × season	2	227	17.39	< 0.001
Area × days since blasting × time period	40	334	2.51	< 0.001
Area × season × days since blasting	16	17,264	41.69	< 0.001
Area × season × time period	20	227	0.66	0.866

^a Full model with all main effects and 3-way interactions.

^b Numerator degrees of freedom.

^c Denominator degrees of freedom from containment method (SAS Institute Inc. 1997).

^d Results from likelihood-ratio Type III *F*-tests (SAS Institute Inc. 1997).

Table 1.3. Significance of random effects from mixed-model ANOVA using restricted maximum likelihood, on activity of female mountain sheep from mined and nonmined areas in the Panamint Range, Inyo County, California, USA, (1995-97).

Source	Z	Pr > Z ^a
Full model ^b		
Season × time period × animal nested within area	7.48	< 0.001
Days since blasting × time period × animals nested within area	4.85	< 0.001
Season models ^c		
Spring; days since blasting × time period × animals nested within area	7.49	< 0.001
Summer; days since blasting × time period × animals nested within area	8.07	< 0.001
Autumn; days since blasting × time period × animals nested within area	6.81	< 0.001

^aSignificance of variance components was tested by determining if

Z-values (component variance divided by SE) differed from zero.

^bFull model with all main effects and 3-way interactions.

^cAll main effects and 3-way interaction since × period × id(area) tested by season.

Table 1.4. Size of home ranges (ha) of mountain sheep from mined and nonmined areas in the Panamint Range, Inyo County, California, USA, (1995-97). *P*-values from 2-sample *t*-test are for within row comparisons of mined versus nonmined.

Home Range Model	Area						
	Nonmined (<i>n</i> = 8)			Mined (<i>n</i> = 7)			<i>P</i>
	\bar{x}	SE	CV	\bar{x}	SE	CV	
Adaptive Kernel							
95%	6,926	834	34	6,222	806	34	0.557
50%	1,230	193	44	954	118	33	0.260
Min. Convex Polygon							
95%	4,006	445	31	3,467	396	30	0.395

Table 1.5. Percent of forage classes in the diets of female mountain sheep, indexed from microhistological analysis of their feces, from mined and nonmined areas in the Panamint Range, Inyo County, California, USA (1995-96).

Area	Percent of forage class ^a							
	Forb		Grass		Shrub		Succulent	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Spring								
Mined (3) ^b	34.4	2.3	1.1	0.6	53.5	2.4	11.1	0.7
Nonmined (3)	26.4	8.3	4.1	0.6	53.9	8.9	15.6	1.0
Summer								
Mined (7)	27.1	3.8	4.5	1.4	59.3	5.1	9.2	1.7
Nonmined (6)	31.0	5.7	5.9	1.0	52.9	4.9	10.3	2.4
Autumn								
Mined (2)	35.4	5.5	1.5	1.5	48.9	3.4	14.3	0.6
Nonmined (4)	31.3	5.2	1.8	1.4	57.5	8.1	9.4	3.8

^aOverall MANOVA (area and season as main effects) was not significant

($F_{8,32} = 1.27$, $P = 0.292$).

^bNumber of composite fecal samples for that season.

Table 1.6. Proportion of young to adult females counted during aerial surveys for mountain sheep near mined and nonmined areas in the Panamint Range, Inyo County, California, USA, (1995-97).

Date					
Area	Lamb (<i>n</i>)	Ewe (<i>n</i>)	<i>P</i> _{<i>i</i>}	95% CI (<i>P</i> _{<i>i</i>})	<i>n</i> Required ^b
Jun 1995 ^a					
Mined	5	7	0.416	0.132-0.700	2,381
Nonmined	6	8	0.428	0.290-0.909	
Oct 1995 ^a					
Mined	1	4	0.200	0.000-0.557	16
Nonmined	11	22	0.333	0.173-0.493	
Jun 1996 ^a					
Mined	4	8	0.333	0.117-0.549	47
Nonmined	5	14	0.260	0.007-0.513	
Jan 1997 ^a					
Mined	3	4	0.428	0.054-0.802	64
Nonmined	2	4	0.666	0.281-1.000	
Oct 1997 ^a					
Mined	3	4	0.428	0.054-0.802	54
Nonmined	3	6	0.333	0.019-0.647	

^aProportion of young to adult females did not differ between areas during that survey as indicated by overlap of 95% confidence intervals.

^bMagnitude of increase in n required to detect a difference in P_i between mined and nonmined areas (e.g., for June 1995, n for young and adult females would have to be multiplied by 2,381 before confidence intervals did not overlap).

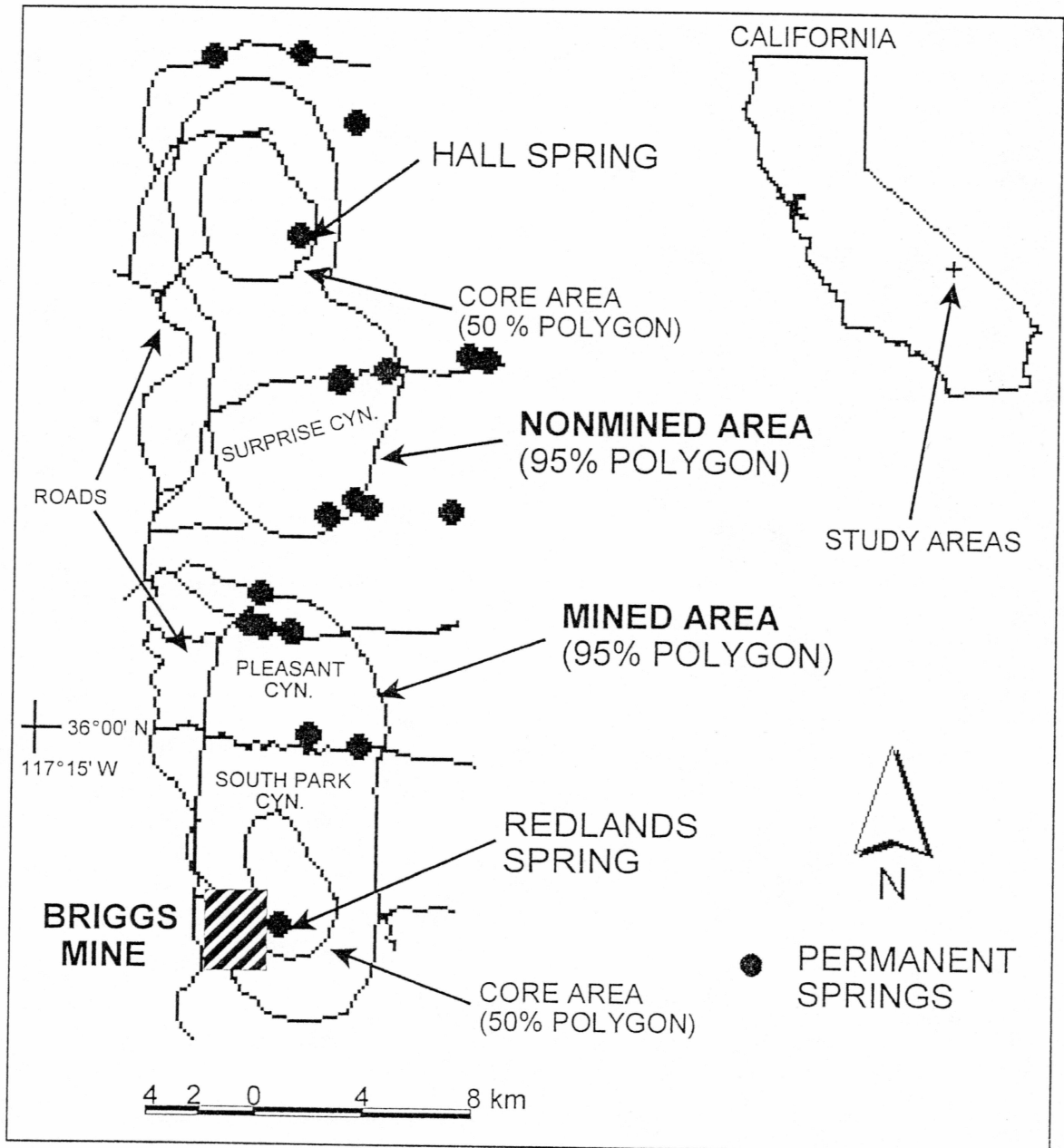


Fig. 1.1. Location of study area, sources of permanent water, other prominent features of the landscape, and 95% adaptive-kernel polygons showing areas used by female mountain sheep in mined and nonmined areas, Panamint Range, Inyo County, California, USA (1995-97).

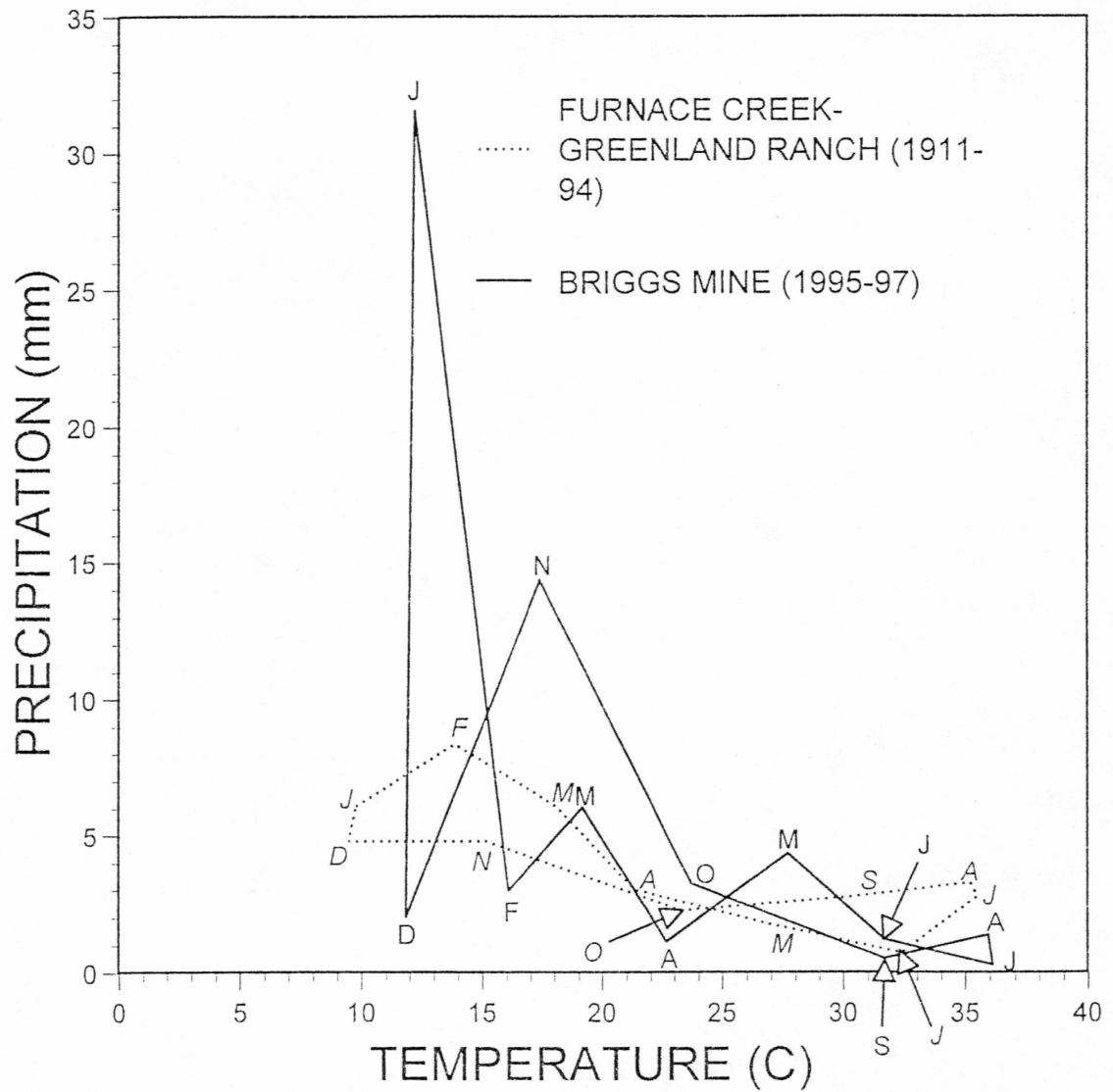


Fig. 1.2. Climograph of mean monthly temperature and precipitation at Briggs Mine (1995-97), and at Furnace Creek-Greenland Ranch (ca.75 km northeast of the Briggs Mine; 1911-94), Inyo County, California, USA.

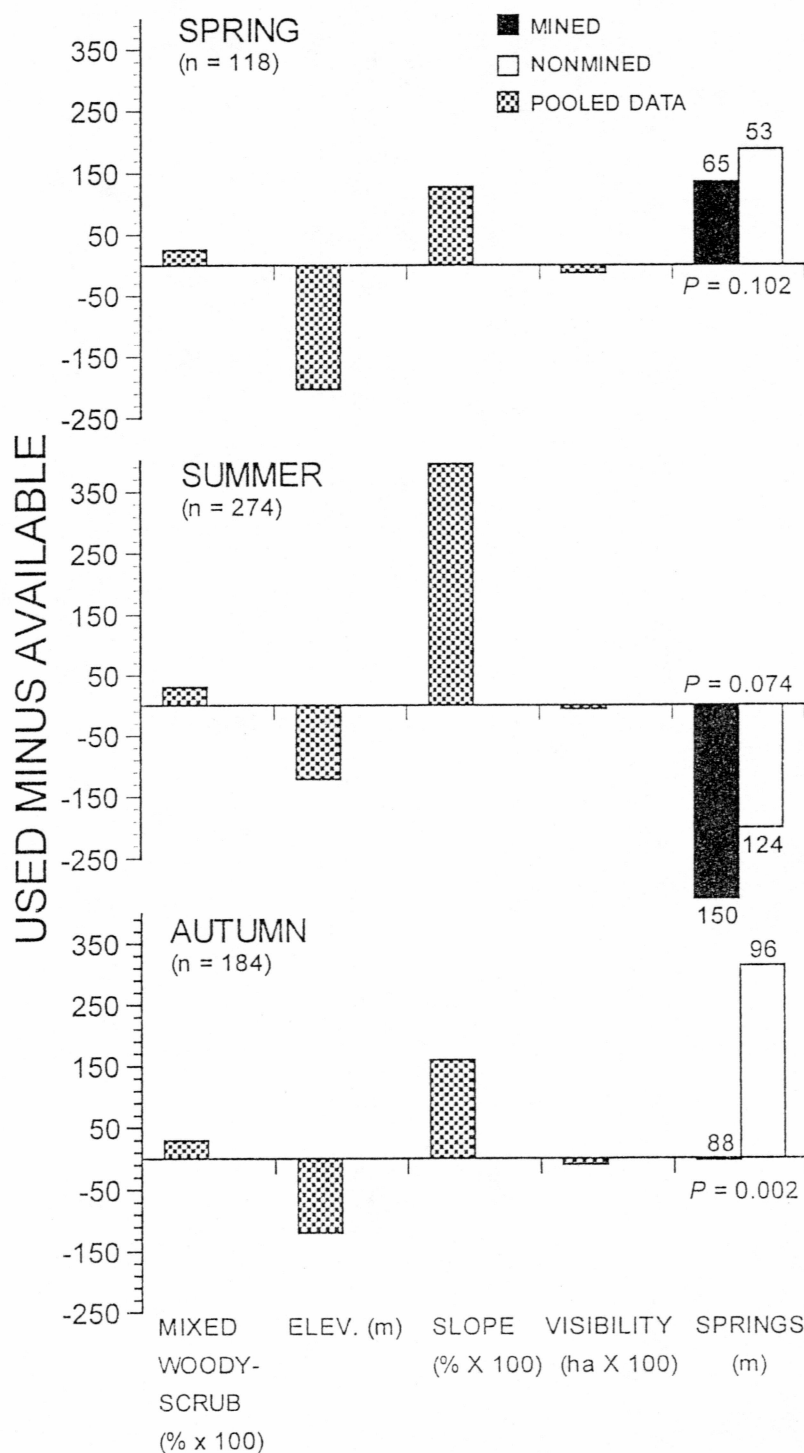


Fig. 1.3. Selection (used minus available) of habitat variables by female mountain sheep in the Panamint Range, Inyo County, California, USA, (1995-97). Numbers by bars represent number of locations sampled.

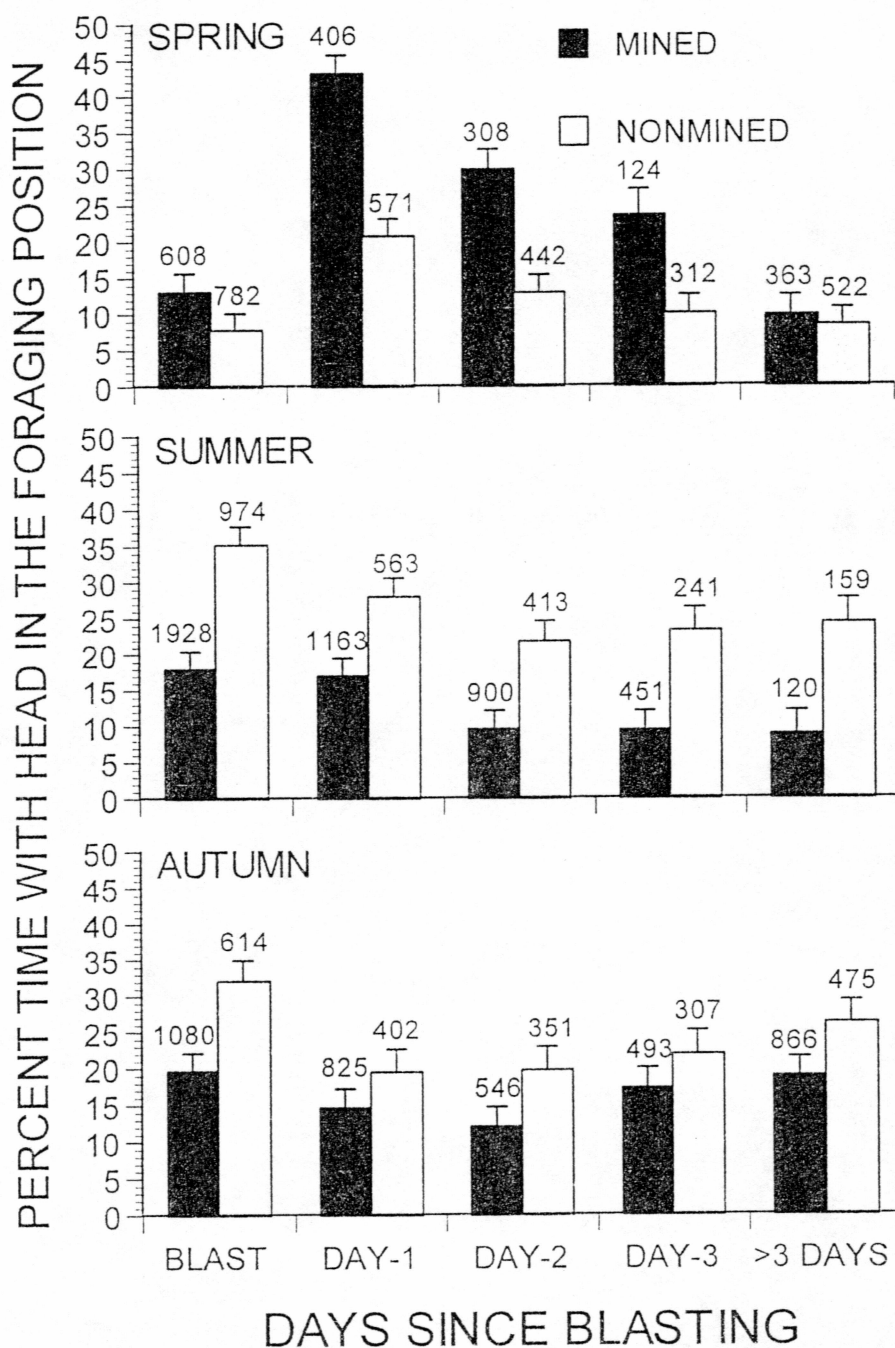


Fig 1.4. Percent time with the head in a foraging position (indexed by tip-switch collar) for female mountain sheep from mined and nonmined areas in the Panamint Range, Inyo County, California, USA (1996-97).

Numbers above bars indicate number of observations.

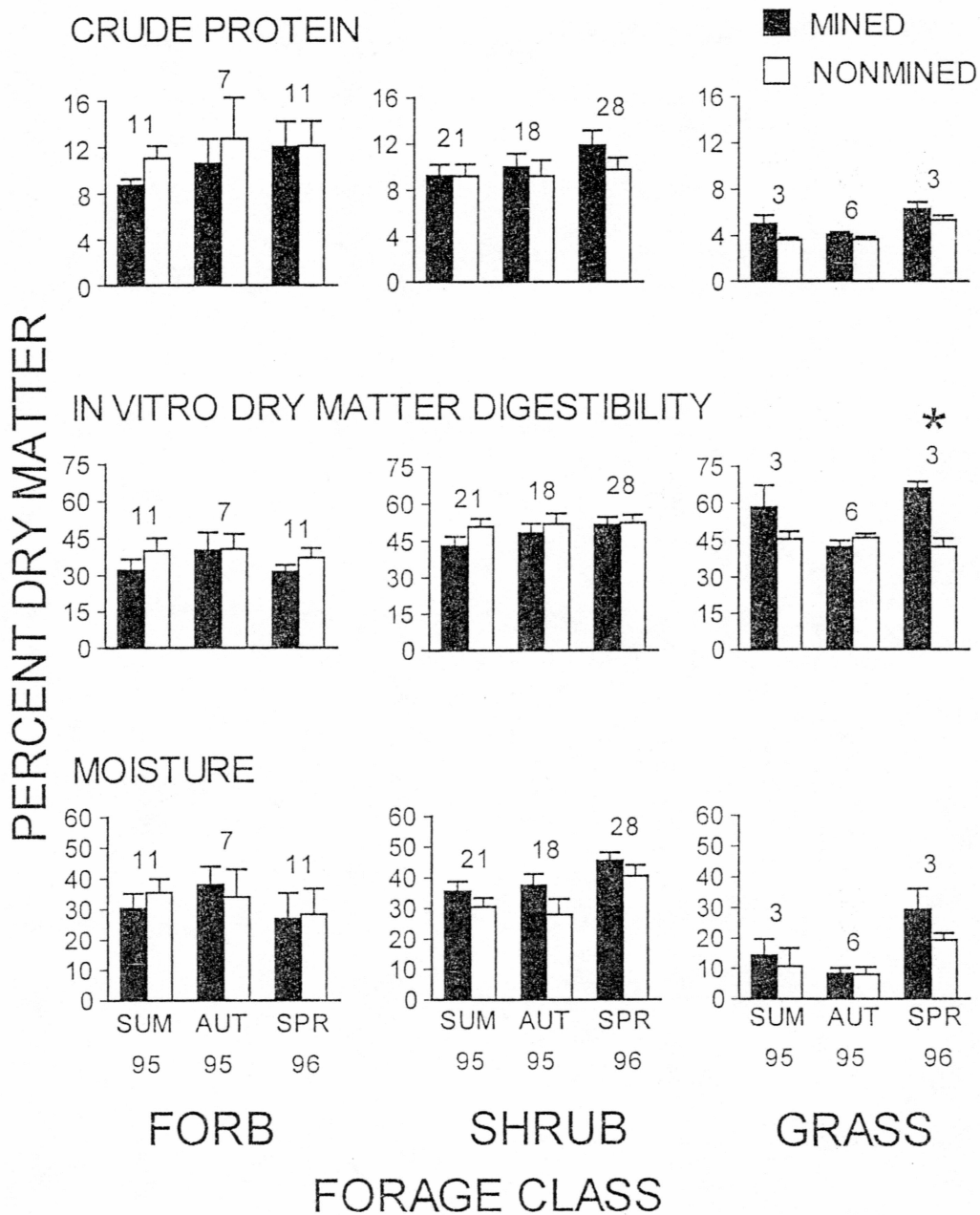


Fig. 1.5 Mean (\pm SE) percent dry matter crude protein (top), *in vitro* dry matter digestibility (middle), and moisture (bottom) content of forages eaten by mountain sheep in the Panamint Range, Inyo County, California, USA (1995-96).

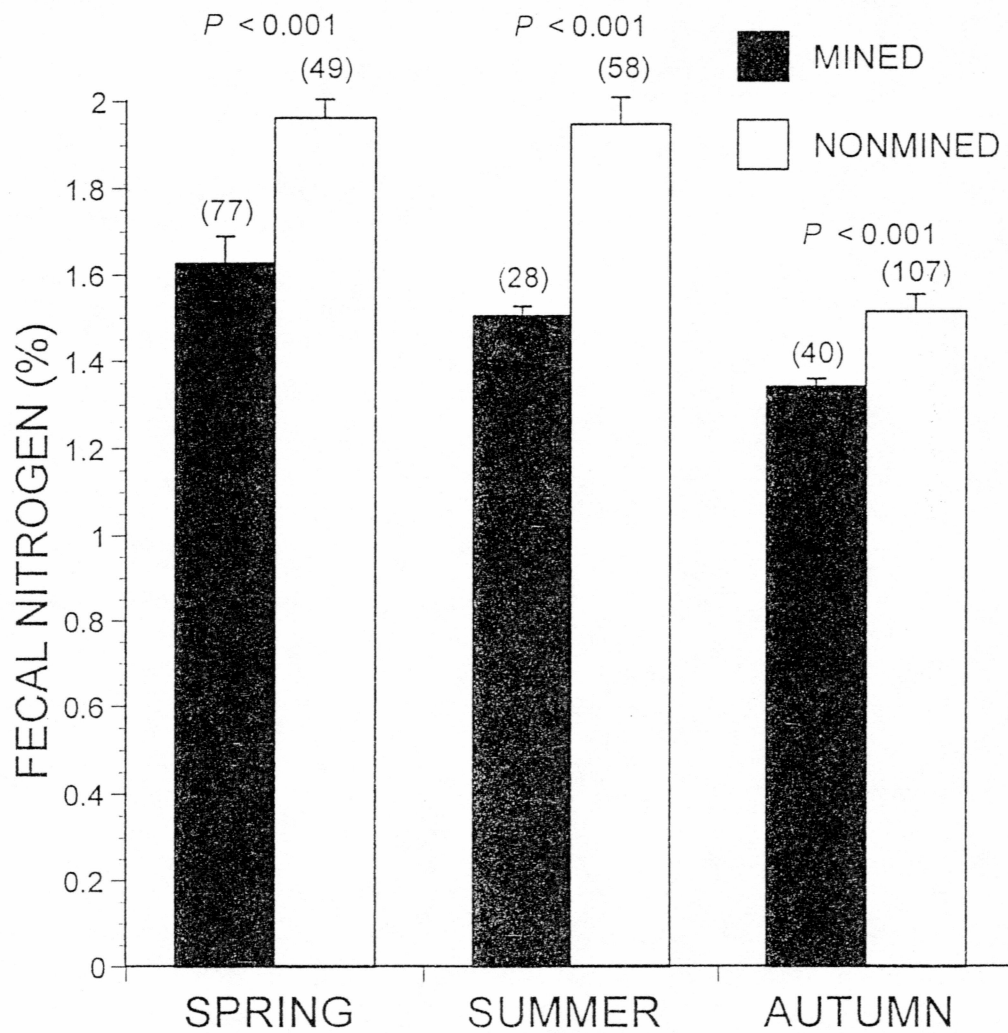


Fig. 1.6. Mean (\pm SE) fecal nitrogen (%) of mountain sheep feces from ranges inhabited primarily by females, from mined and nonmined areas in the Panamint Range, Inyo County, California, USA (1995-97).

Number above bars represent sample size.

CHAPTER 2.

HOME RANGES OF MOUNTAIN SHEEP:

EFFECTS OF PRECIPITATION IN A DESERT ECOSYSTEM

We compared sizes of home ranges and other ecological variables for female mountain sheep (*Ovis canadensis nelsoni*) inhabiting geographically and climatologically distinct areas in the Mojave Desert of southeastern California. We also examined the relation between size of home range and body size of mountain sheep. Precipitation in the more xeric Panamint Range was uni-modal, with a modest peak in winter, whereas rainfall at less xeric Old Dad Peak was bi-modal, with peaks in summer and winter. Monthly precipitation was more variable in the Panamint Range than at Old Dad Peak. Density of female sheep was about four times greater at Old Dad Peak than in the Panamint Range, which was typified by more bare ground, fewer shrubs, and fewer perennial grasses than at Old Dad Peak. Sizes of 95% adaptive-kernel home ranges and core areas (50%) were nearly twice as large for female mountain sheep inhabiting the drier Panamint Range, but females from Old Dad Peak occurred nearer water than mountain sheep in the Panamint Range. We detected no relations between size of body or age and home-range size for female mountain sheep. Additionally, no differences occurred between areas in either body size or horn size. Female mountain sheep from Old Dad Peak foraged predominantly on grasses and forbs, whereas those from the Panamint Range consumed mostly shrubs and forbs, and to a lesser extent, succulents. In general, quality of forage was higher at Old Dad Peak than in the Panamint Range. Diet quality (as indexed by fecal nitrogen) did not differ between areas in spring, but was higher in the Panamint Range during summer and autumn, perhaps because of higher population density of mountain sheep at Old Dad Peak. We conclude that mountain

sheep from the Panamint Range had larger home ranges than those from near Old Dad Peak because of lower availability and quality of forage, a consequence of the precipitation regime. Use of cacti in the Panamint Range likely enhanced the ability of females to go without free-water, and thereby increased the area in which they could forage in that depauperate and more xeric environment. We hypothesize that pattern and amount of precipitation and subsequent productivity of plants can affect probabilities of persistence for populations of mountain sheep.

Key words: *Ovis canadensis nelsoni*, mountain sheep, body size, home range, horns, diet, precipitation, water, climatic variability, population persistence, southeastern California

Life-history strategies of ungulates often involve tradeoffs between acquiring forage and avoiding predators (Bowyer et al., 1998a, 1999; Kie, 1999). Likewise, climatic variability is thought to play a critical role in shaping the adaptations of these large herbivores to the environments they inhabit (Bowyer, 1991; Bowyer et al., 1998b; Post et al., 1997). Environmental constraints are especially important for wild populations of *Ovis* in North America (Bunnell, 1992; Rachlow and Bowyer, 1991, 1994, 1998). Timing and amount of precipitation in desert ecosystems regulate primary production (Beatley, 1974a, 1974b) and the ability of large herbivores to cope physiologically with such xeric environments (Mousa et al., 1983; Turner, 1973).

Many authors have related the sizes of home ranges of ungulates to factors such as body size, sex, age, and availability of resources (Cederlund and Sand, 1994; du Toit, 1990; Hundertmark, 1998; Krausman et al., 1989; Larter and Gates, 1994). In general, size of home range increases with body size, both among (Swihart et al., 1988) and within taxa (du Toit, 1990), and is usually larger for males of dimorphic species (Cederlund and Sand, 1994; Krausman et al., 1989). Further, home ranges are larger where resources are

limited (Krausman et al., 1989; Leslie and Douglas, 1979). McNab (1963) suggested that because precipitation influenced the distribution and abundance of plants, the amount of precipitation also should determine the extent of area that has to be searched by a herbivore to acquire nutrients. Indeed, compelling evidence exists that the timing and amount of precipitation are critical factors determining productivity in desert ecosystems (Beatley, 1974a, 1974b; Went, 1949). Hence, precipitation should be a factor in determining size of home ranges for animals occupying those hot, dry ecosystems, with larger home ranges for mammals living in more arid environments than those inhabiting less xeric ones.

We reasoned that because of the disparate patterns of precipitation between the eastern and northern Mojave desert in California (Bleich et al., 1997; Welles and Welles, 1961), the ecology of mountain sheep (*Ovis canadensis nelsoni*) occupying those dissimilar yet nearby areas likewise should differ. We hypothesized that sizes of home ranges would be larger for female sheep inhabiting the Panamint Range, where total precipitation was lower and occurred less frequently than near Old Dad Peak (Figs. 2.1a and 2.1b). As a consequence of less precipitation in the Panamint Range, we also predicted that quantity (Beatley, 1974b) and quality of forage would be lower in that area and, consequently, so too would quality of diets of females (Wehausen and Hansen, 1988). We further hypothesized that female mountain sheep inhabiting Old Dad Peak would occur farther from sources of permanent water than those in the more xeric Panamint Range.

Warrick and Krausman (1989) suggested that desert-dwelling mountain sheep may augment water intake by increasing use of succulents (i.e., cacti) in extremely xeric areas. Wehausen (1991) reported that female sheep inhabiting areas with abundant barrel

cactus (*Ferocactus acanthodes*) possessed horns with larger basal diameters than those in areas without that resource. He reasoned that larger horns would enable sheep to break open cacti with a lower risk of injury and resultant avenues for infection. Thus, we tested for differences in horn size of females between areas to assess potential relationships between horn morphology and the ecology of these desert sheep. We also tested whether females with differing body size would exhibit variability in the size of their home ranges (sensu Swihart et al., 1988). Finally, we discuss climatic variation and population demography in relation to the conservation of these unique desert ungulates.

MATERIALS AND METHODS

Study areas.—Our study area in the northern Mojave Desert, which exhibited a unimodal pattern of precipitation (Fig. 2.1a), was located near Death Valley National Park on the west-facing scarp of the Panamint Range, Inyo Co., California, (36°00'N, 117°10'W). We defined three seasons: spring (1 January-30 April); summer (1 May-31 August); and autumn (1 September-31 December) based on patterns of precipitation, temperature, and life-history characteristics of mountain sheep (Bleich et al., 1997).

Elevations in the Panamint Range varied from 305 m on the valley floor to 3,370 m at the summit of Telescope Peak. Precipitation from 1948 to 1989 at Greenland Ranch-Furnace Creek, California (ca. 60 km northeast of the study site) exhibited a unimodal pattern. Average annual precipitation was 51 mm with about one-half occurring from January to March, and the rest falling sporadically during the remainder of the year (Fig. 2.1a). Data collected on the study area from 1995 to 1997 revealed a similar pattern of precipitation during summer, but showed a marked increase in precipitation in winter (particularly in January; Fig. 2.1b). The peak in January illustrated extreme variability in precipitation; 99% of total precipitation in January for 1995-1997 fell during 1995, none

occurred in 1996, and the rest fell during 1997. Temperature was highly variable and ranged from 40°C during summer to -7°C in spring.

Plant communities in the Panamint Range were described by T. Ginnett and C. Douglas (in litt.). Briefly, a creosote bush-scrub (*Larrea tridentata*) community, interspersed with desert washes, occurred on the valley floor and alluvial areas. Shadscale-scrub (*Atriplex confertifolia*) occupied areas between 1,400-2,300 m elevation, and was dominated by shadscale and blackbrush (*Coleogyne ramosissima*). Above the shadscale-scrub was the sagebrush community with black sagebrush (*Artemisia nova*) and *Chrysothamnus* dominating. Upper elevations (>2,500 m) were characterized by pinyon pine (*Pinus monophylla*) and juniper (*Juniperus osteosperma*). Mesquite (*Prosopis glandulosa*) was common in moist canyons throughout the area.

Twenty-one permanent springs occurred within areas inhabited by female mountain sheep in the Panamint Range. That area possessed a full complement of large mammalian predators including coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and mountain lions (*Puma concolor*), but predation on mountain sheep by those carnivores is uncommon (Welles and Welles, 1961). Other ungulates present in the Panamint Range included feral asses (*Equus asinus*) and, less commonly, mule deer (*Odocoileus hemionus*). Based on helicopter surveys during 1995-1997, adult female sheep occurred on this range at a density of about 72/1,000 km²; the ratio of young:adult female was 0.43:1.

Data on female mountain sheep from the eastern Mojave Desert (bi-modal pattern of precipitation) were obtained from Bleich (1993) and Bleich et al. (1992, 1997). Those data were collected in an area that encompassed Old Dad Peak, Cowhole Mountain, and the Kelso and Marl mountains in San Bernardino Co., California (35°05'N, 115°45'W),

hereafter referred to as Old Dad Peak. Elevations ranged from 300 m in the inter-mountain areas to 1,466 m at Kelso Peak. Precipitation at Twentynine Palms, California (ca. 70 km southwest of the study area) during 1948-1989 was bi-modal; average annual precipitation was 101 mm (Fig. 2.1a). A similar pattern of precipitation was observed at Baker, California (30 km northeast of the study area), with about one-half occurring as localized summer thundershowers and the other half falling during December-March (Fig. 2.1b). Daytime maxima in summer normally exceeded 38°C, and temperatures below freezing during spring were not uncommon (Bleich et al., 1997). Vegetation types were from Martens and Baldwin (1983) and descriptions of dominant species followed Bleich (1993): creosote-bush scrub-creosote bush, burro-weed (*Ambrosia dumosa*); desert-wash-cheese-weed (*Hymenoclea salsola*), white brickellbush (*Brickellia incana*); *Yucca-Ephedra* scrub-creosote bush, ephedra (*Ephedra*); sand dunes-big galleta (*Hilaria rigida*); and, rupicolus scrub-burro-weed, creosote bush. There were six natural and four artificial sources of water (Bleich et al., 1997).

Carnivores inhabiting Old Dad Peak included bobcats, mountain lions, and coyotes. Mule deer occurred infrequently within the study area, but feral asses and domestic cattle were common (Bleich et al., 1997). From 1988 to 1990, density of adult female mountain sheep was estimated at 270/1,000 km², and the ratio of young:adult female was 0.29:1 (Jaeger et al., 1991). Additionally, 155 adult female sheep were removed from that mountain complex from 1983 to 1989 for translocation (Bleich et al., 1990a).

Sampling procedures and statistical analyses.—To characterize and examine potential differences in patterns of precipitation between study areas, we used long-term data (Fig. 2.1a) on weather from Greenland-Ranch Furnace Creek (1948-1989), and

Twentynine Palms (1948-1989). Those sites were chosen because of their proximity to our study areas and their concordant dates. Data from sites nearer our study areas (Baker, and Redlands Canyon; Fig. 2.1*b*) were compared with long-term data. We used one-way analysis of variance (ANOVA), with area as the main effect and mean monthly precipitation as the dependent variable, to compare Greenland-Ranch Furnace Creek and Twentynine Palms. Because the timing and amount of precipitation and plant responses are closely correlated (Beatley, 1974*b*), we also compared the mean number of years between periods when >25 mm of precipitation fell with a *t*-test. We evaluated coefficients of variation (*CV*) between areas with a sign test (Siegel, 1956). We did not evaluate differences in temperature between study areas because precipitation is a much better index to plant abundance in those hot desert ecosystems (Beatley, 1974*a*).

Female mountain sheep were captured in the Panamint Range ($n = 19$) between June 1995-January 1997, and at Old Dad Peak ($n = 17$) from September 1986 to June 1990 by personnel of the California Department of Fish and Game with a helicopter and a hand-held net-gun (Krausman et al., 1985). Those mountain sheep were fitted with telemetry collars (Telonics, Mesa, AZ or Advanced Telemetry Systems, Isanti, MN) following the recommendations of Bleich et al. (1990*b*), and age was determined with horn-growth rings (Geist, 1968) or patterns of tooth replacement (Deming, 1952). At Old Dad Peak, females radiocollared for telemetry studies were not weighed or measured because of logistical constraints; however, an additional 155 female mountain sheep from that area were weighed to the nearest 0.5 kg; chest girth was measured to the nearest 1 cm (Bleich et al., 1997). Additionally, circumference at the base of each horn was measured to the nearest 1 mm. For females captured in the Panamint Range, only chest girth and horn measurements were recorded; therefore, we used data from females captured at Old

Dad Peak to develop a regression model to evaluate chest girth as a potential surrogate for body mass. We used the Mann-Whitney test to compare chest girths and ages between study areas, and analysis of covariance (ANCOVA) with age as the covariate to examine potential differences in size of horns between study areas. All aspects of animal handling complied with protocols set forth by Jessup et al. (1986), and were consistent with methods adopted by the American Society of Mammalogists (Animal Care and Use Committee, 1998). No deaths resulted from our capture efforts, and predation was an unimportant source of mortality for females in both study areas; one female was killed by a mountain lion in the Panamint Range.

Radiocollared mountain sheep were located with a fixed-wing aircraft (Krausman et al., 1984) approximately once each week from October 1986 to December 1990 at Old Dad Peak. In the Panamint Range, sheep were located weekly during June-August, and every other week for the remainder of the year from 1995 to 1997. We estimated locations of collared sheep with LORAN-C or a global positioning system (GPS) aboard the aircraft. Because of error inherent with LORAN-C (Jaeger et al., 1993; Oehler et al., 1996), we corrected locations obtained with that method (Patric et al., 1988). Because GPS is less subject to geographic variability in accuracy than LORAN-C (Leptich et al., 1994), we did not correct locations obtained with that technology. We used a geographic information system (GIS; ARC/INFO, Environmental Systems Research Institute, Redlands, CA) to determine the distances from locations of mountain sheep and random locations to sources of permanent water. Because availability of water differed between areas, we determined the mean difference between the distances from water that radiocollared female sheep and equal numbers of random locations occurred. We used two-way ANOVA (area and season as main effects, and mean difference as the dependent

variable) to analyze those data (Bleich et al., 1997).

We used the multiresponse sequence procedure (MRSP) of BLOSSOM statistical software (Slauson et al., 1991; Solow, 1989) to test locations within each data set for lack of independence (Swihart and Slade, 1985). Prior to calculating adaptive-kernel home ranges for each animal, we used CALHOME (Kie et al., 1996) to estimate the parameter for the optimum smoothing of the 95% adaptive kernel (Worton, 1989, Kie et al., 1996). Next, we calculated 95% adaptive-kernel home ranges based on 60-120% of that smoothing parameter; the value that minimized the least squares cross-validation score for each data set was then used as the smoothing parameter for that particular female when calculating adaptive-kernel home ranges (Kie et al., 1996).

We estimated sample size necessary to compute home ranges with the nonlinear procedure in SPSS (Statistical Package for the Social Sciences, 1993). We eliminated data sets that did not attain 90% of that asymptotic value from further analyses (Nicholson et al., 1997). We determined that size of home ranges of sheep attained 90% of the asymptote at sample sizes ($\bar{X} \pm SD$) of 39.8 ± 13.9 locations at Old Dad Peak, and 26 ± 6.7 locations in the Panamint Range. We tested hypotheses regarding home-range size with data from seasons combined because of inadequate sample size within seasons. We used 95% adaptive kernels to estimate overall size of home ranges, and the 50% isopleth as our measure of core areas (Bertrand et al., 1996); 95% minimum convex polygons (MCPs) were presented for comparison with other studies. Mean sizes of home ranges were compared with a *t*-test (Zar, 1999).

We examined the relationship between size of home range and chest girth, and median age of each individual, using simple linear regression (Zar, 1999). We used data from female sheep from both study areas (Panamint Range, $n = 13$; Old Dad Peak, $n =$

15) to explore the relationship between size of home range and age. Because we did not have data on chest girth and home range for the same individuals from Old Dad Peak, size of home range and chest girth were examined with data only from the Panamint Range ($n = 13$).

We quantified vegetation on randomly located step-point transects (Bowyer and Bleich, 1984) to compare relative abundance of forage between study areas. We used multivariate analysis of variance (MANOVA) and univariate F -tests to examine potential differences in the proportions of vegetation cover between areas. We also evaluated the abundance of shrubs using a linear regression model (percent cover of shrubs = $0.10 \times$ precipitation in mm + 3.96; $r^2 = 0.83$) developed by Beatley (1974a) to predict cover of shrubs in the Mojave Desert. Plant nomenclature followed Munz (1974).

Nitrogen content of forage collected in the Panamint Range was determined with a Leco CNS-2000 Elemental Analyzer (Leco Corporation, St. Joseph, MO), whereas those at Old Dad Peak were estimated with micro-Kjeldahl digestion; data were pooled by area, forage class, and season (Bleich et al., 1992). We analyzed crude protein, *in vitro* dry matter digestibility (IVDMD; Van Soest, 1994), and percent moisture (dependent variables) separately with three-way ANOVA with study area, season, and forage class as main effects.

We used data from fecal groups composited by month in the Panamint Range (25 months, 359 fecal groups), and 122 individual fecal groups, collected over 24 months, from Old Dad Peak to index composition of the diet of female mountain sheep. Composition of plant species in fecal groups from both areas was determined at the Forage Analysis Laboratory, University of Arizona (Tucson, AZ), with the microhistological techniques described by Sparks and Malechek (1968). Plant fragments

were categorized as forbs, grasses, shrubs, or succulents. Composition of diet was analyzed with a two-way MANOVA with forage classes as dependent variables, and study area and season as main effects.

We used fecal nitrogen (FN) as an index to quality of diet. We determined FN on individual pellet groups (Old Dad Peak, $n = 122$; Panamint Range, $n = 359$) and pooled those data by area and season. We tested the relationship between FN and the percentage of shrubs in diets (considered to be the primary source of phenolics) using linear regression (Zar, 1999) to determine if our results on FN may have been confounded. To correct fecal nitrogen for potential differences in inorganic compounds in feces, we used a muffle furnace (Van Soest, 1994) to ash a randomly selected sub-sample of fecal groups from Old Dad Peak ($n = 25$) and the Panamint Range ($n = 36$). Ash contents of fecal samples from the Panamint Range were 16.3, 18.0, and 16.2% during spring, summer, and autumn, respectively, whereas those from Old Dad Peak were 23.7, 21.7, and 23.1% during those same seasons. We used the mean ash content for a particular season and area to correct other such samples, and compared percent FN of corrected samples with a two-way ANOVA, with area and season as class variables, and FN as the dependent variable.

We examined assumptions of each statistical test and transformed data as necessary. When multi-factor ANOVA was employed, we evaluated all individual factors and their interactions; significant models ($P \leq 0.05$) were further explored using Tukey's honestly significant difference (HSD; Zar, 1999). We used a Bonferroni correction (Kleinbaum et al., 1988) to control for experiment-wide error when conducting multiple comparisons, and bivariate correlations were evaluated with a Pearson product-moment correlation (Zar, 1999). We report all values as means ± 1 SD unless otherwise

indicated, and adopted $\alpha = 0.05$. We analyzed data with PC SAS (SAS Institute Inc., 1997) and SPSS (Statistical Package for the Social Sciences, 1993).

RESULTS

Precipitation.—ANOVA revealed mean monthly precipitation was greater at Old Dad Peak than the Panamint Range during July-October, and during December (Fig. 2.1a). Nonetheless, monthly variation (CV) was significantly more variable (sign test, $P < 0.002$) in the Panamint Range ($\bar{X} = 191\%$, $SD = 46\%$) than at Old Dad Peak ($\bar{X} = 165\%$, $SD = 34\%$) in 11 of 12 months. This same pattern held when the critical period (September-December) was considered—precipitation in the Panamint Range was more variable. In the Panamint Range, 10 years occurred between 1948-1989 when >25 mm of precipitation fell during September-December, whereas 14 such years occurred at Old Dad Peak. Mean ($\pm SD$) number of years between periods when >25 mm of precipitation occurred did not differ ($t = 0.74$, $d.f. = 20$, $P = 0.70$) between areas (Panamint Range, 2.3 ± 1.6 years; Old Dad Peak, 1.8 ± 1.8 years).

Morphometrics.—Our regression model indicated that chest girth provided a reliable index to body mass (Fig. 2.2). Mean ($\pm SD$) chest girth of female mountain sheep from Old Dad Peak was 85.8 ± 8.6 cm, and was 88.9 ± 5.9 cm for females in the Panamint Range; no significant difference occurred between study areas ($U = 961$, $P = 0.14$). Basal circumference of horns was 14.9 ± 1.9 cm for 18 females from the Panamint Range, and 14.7 ± 1.7 cm for 53 females from Old Dad Peak; again, no difference existed between areas ($F = 1.34$, $d.f. = 2, 70$, $P = 0.252$).

Home-range size.—We used data on locations from 15 female mountain sheep each from Old Dad Peak and the Panamint Range to compare sizes of home ranges. Mean size of home range estimated with 95% adaptive kernel was significantly larger for females

inhabiting the Panamint Range than for those from Old Dad Peak (Table 2.1). Likewise, 50% adaptive-kernel home ranges also were significantly larger for females in the Panamint Range than those at Old Dad Peak (Table 2.1). Sheep from Old Dad Peak exhibited more variability in home-range size than those from the Panamint Range (Table 2.1).

Mean (\pm *SD*) age of 13 radiocollared female mountain sheep from the Panamint Range was 4.7 ± 1.9 years, whereas mean age of 15 females from Old Dad Peak was 6.0 ± 2.1 years; no significant difference occurred between areas ($U = 75.0$, $P = 0.28$). When sizes of home ranges for females from the Panamint Range were regressed on chest girth, little variation was explained ($r^2 = 0.05$, $P = 0.44$). Similarly, regressions of size of home ranges on age for females from both study areas explained little variation in size of home range (Fig 2.3).

Distance to water.—After controlling for availability of water, female sheep at Old Dad Peak were located significantly nearer water than females from the Panamint Range during all seasons (spring, $F = 39.76$, $d.f. = 1, 309$, $P < 0.001$; summer, $F = 124.06$, $d.f. = 1, 523$, $P < 0.001$; autumn, $F = 10.35$, $d.f. = 1, 309$, $P < 0.001$; Table 2.2). Tukey's HSD test revealed that distance to water did not differ ($P > 0.05$) among seasons for females from the Panamint Range. Similarly, distance from female sheep to water did not differ between spring and summer at Old Dad Peak ($P > 0.05$), but sheep were significantly nearer water during those seasons than during autumn ($P \leq 0.05$; Table 2.2).

Forage abundance.—Significant differences occurred in proportions of vegetative cover between areas used by female mountain sheep from the Panamint Range and those at Old Dad Peak (Fig. 2.4). Ranges inhabited by female sheep at Old Dad Peak had greater cover of shrubs, perennial forbs, and perennial grasses than did areas occupied by

females in the Panamint Range (Fig. 2.4); in contrast, the Panamint Range was typified by more bare ground. Shrub cover predicted from the model of Beatley (1974a) was 8.7% for the Panamint Range, and 12.0% for Old Dad Peak, and was ca. 20% less than data from transects we sampled (10.7% in Panamint Range, and 15.2% at Old Dad Peak).

Forage quality.—When area, season, and forage class were considered in a three-way ANOVA, significant differences occurred among mean levels of crude protein in forage ($F = 7.83$, $d.f. = 17, 580$, $P < 0.001$; Table 2.3). That outcome was influenced by the highly significant effect of forage class ($F = 44.89$, $d.f. = 2, 580$, $P < 0.001$) and, to a lesser extent, differences between seasons ($F = 3.53$, $d.f. = 2, 580$, $P = 0.03$). When two-way ANOVAs (area and forage class) were conducted by season, all models were highly significant (spring, $F = 6.77$, $d.f. = 5, 199$, $P < 0.001$; summer, $F = 8.56$, $d.f. = 5, 194$, $P < 0.001$; autumn, $F = 10.34$, $d.f. = 5, 185$, $P < 0.001$). Again, those outcomes were the result of significant effects of forage class during all seasons (spring, $F = 11.95$, $d.f. = 2, 199$, $P < 0.001$; summer, $F = 14.72$, $d.f. = 2, 194$, $P < 0.001$, autumn, $F = 24.31$, $d.f. = 2, 185$, $P < 0.001$). During spring, there were no significant differences between areas in crude protein of the 3 forage classes, whereas in summer, crude protein of perennial forbs and perennial grasses was higher at Old Dad Peak than in the Panamint Range; shrubs did not differ during that season (Table 2.3). In autumn, no significant differences occurred in crude protein of perennial forbs and shrubs between areas, but perennial grasses had more protein at Old Dad Peak than in the Panamint Range during that season (Table 2.3).

In the Panamint Range, no differences occurred in crude protein among forage classes during spring ($F = 2.38$, $d.f. = 2, 83$, $P = 0.10$), whereas at Old Dad Peak crude protein was higher (HSD test) in perennial forbs than shrubs ($P \leq 0.05$), which in turn, was higher than perennial grasses ($P \leq 0.05$). In summer and again in autumn, crude

protein of perennial forbs and shrubs did not differ ($P > 0.05$) in the Panamint Range; however, both crude protein content of perennial forbs and shrubs were higher than that of perennial grasses in that range during both of those seasons ($P \leq 0.05$). At Old Dad Peak, perennial forbs and shrubs did not differ significantly in protein content ($P > 0.05$) during any season, but both were higher than protein content of perennial grasses ($P \leq 0.05$) during summer and autumn.

When IVDMD of forage was considered by area, season, and forage class in a three-way ANOVA, a highly significant difference was obtained ($F = 4.08$, $d.f. = 17, 580$, $P < 0.001$; Table 2.3). That outcome was influenced by the significant area by forage class interaction ($F = 18.33$, $d.f. = 2, 580$, $P < 0.001$). During spring, 1-way ANOVA indicated that perennial grasses and shrubs were more digestible in the Panamint Range than at Old Dad Peak ($P \leq 0.05$), whereas perennial forbs were more digestible at Old Dad Peak during that season (Table 2.3). In summer, perennial forbs were more digestible at Old Dad Peak ($P \leq 0.05$), perennial grasses were more digestible in the Panamint Range ($P \leq 0.05$), and digestibility of shrubs did not differ between areas (Table 2.3). In autumn, digestibility did not differ within any of the forage classes when they were compared by area (Table 2.3).

Three-way ANOVA indicated significant seasonal variation in amount of moisture in forage within and between study areas, as well as between forage classes ($F = 41.52$, $d.f. = 17, 2200$, $P < 0.001$; Table 2.3). When two-way ANOVAs were conducted by season (area and forage class as main effects), all models were highly significant (spring, $F = 25.19$, $d.f. = 5, 744$, $P < 0.001$; summer, $F = 33.60$, $d.f. = 5, 725$, $P < 0.001$; autumn, $F = 74.59$, $d.f. = 5, 729$, $P < 0.001$). After correcting for multiple comparisons, no significant differences occurred in moisture content of perennial forbs between Old

Dad Peak and the Panamint Range during any season (Table 2.3). Moisture content of perennial grasses did not differ between areas during spring, but was significantly higher at Old Dad Peak than in the Panamint Range during summer and autumn (Table 2.3). Finally, moisture content of shrubs was significantly higher at Old Dad Peak than in the Panamint Range during all seasons (Table 2.3). Within the Panamint Range, moisture content was significantly greater for shrubs than for perennial grasses or perennial forbs during spring ($P \leq 0.05$), but moisture content of perennial forbs and perennial grasses did not differ ($P > 0.05$) during that season. During summer and autumn, moisture content of perennial forbs and shrubs did not differ in the Panamint Range ($P > 0.05$), but moisture content of both were higher than for perennial grasses ($P \leq 0.05$). At Old Dad Peak, perennial forbs and shrubs had significantly more moisture than did perennial grasses during spring and autumn ($P \leq 0.05$), but did not differ from each other during those seasons ($P > 0.05$). In summer, moisture content of perennial forbs and perennial grasses did not differ at Old Dad Peak, but both were significantly less than for shrubs ($P \leq 0.05$).

Diet composition.—Overall, diets of female mountain sheep from Old Dad Peak were composed of 38% forbs, 35% grasses, 26% shrubs, and 1% succulents, whereas females in the Panamint Range consumed 30% forbs, 4% grasses, 55% shrubs, and 11% succulents (Table 2.4). Substantial differences in the composition of diets of female sheep occurred between study areas ($F = 2.61$, $d.f. = 8, 276$, $P = 0.009$; Table 2.4). Because one-way MANOVAs (area as main effect) conducted by season were all highly significant (spring, $F = 60.60$, $d.f. = 4, 41$, $P < 0.001$; summer, $F = 52.08$, $d.f. = 4, 56$, $P < 0.001$; autumn, $F = 5.58$, $d.f. = 4, 35$, $P = 0.001$), we used one-way ANOVA (area as the main effect) for each forage class and season to test for differences between areas (Table

2.4).

Quality of diet.—Two-way ANOVA (area and season) indicated significant differences in FN ($F = 15.56$, $d.f. = 5, 480$, $P < 0.001$); however, those differences were influenced to a greater extent by season ($F = 31.04$, $d.f. = 2, 580$, $P < 0.001$) than by differences between areas ($F = 4.48$, $d.f. = 1, 580$, $P = 0.035$). HSD tests revealed that FN in the Panamint Range was greater during spring than summer ($P \leq 0.05$), and spring and summer were both greater than autumn ($P \leq 0.05$). Similarly, FN at Old Dad Peak was greater during spring and summer than in autumn ($P \leq 0.05$); however, FN did not differ during spring and summer ($P > 0.05$). FN was not significantly different between areas during spring, but was higher in the Panamint Range during summer and autumn (Fig. 2.5).

In general, diet quality was highest for both areas during spring, decreased during summer, and was lowest during autumn (Fig. 2.5). Perhaps protein-complexing phenolics associated with shrubs confounded our results of FN; however, that was unlikely because there was no association between FN and proportion of shrubs in diets for mountain sheep in either the Panamint Range ($r^2 = -0.243$, $P = 0.24$) or at Old Dad Peak ($r^2 < 0.001$, $P = 0.91$).

DISCUSSION

Long-term monthly precipitation was less in the Panamint Range than at Old Dad Peak (Fig. 2.1a). Most noteworthy for both the long- (Fig. 2.1a) and short-term (Fig. 2.1b) data was the lack of precipitation near the Panamint Range in summer, and the pronounced peak in precipitation near Old Dad Peak during that season. Moreover, precipitation was more variable in the Panamint Range than at Old Dad Peak in 11 of 12 months from 1948 to 1989. Precipitation events, however, can be extremely variable and

localized in desert ecosystems, and differences in precipitation between even nearby locations can be large (Beatley, 1974a; Went, 1949). Short-term precipitation reflected longer-term patterns (Fig. 2.1a and 2.1b), but was less concordant for the Panamint Range than at Old Dad Peak, an outcome consistent with greater variability in that more xeric system. Differences in climate during the course of our study (Fig. 2.1b) from long-term patterns (Fig. 2.1a) may have had two effects: 1) an underestimation of annuals at Old Dad Peak because of drought; and 2) perhaps an increase in annual plants in the Panamint Range following high precipitation during January 1995. These short-term aberrations would not affect the distribution of shrubs (Beatley, 1974a; Went, 1949), or perhaps perennial grasses and perennial forbs.

The broad pattern of precipitation (e.g., uni-modal or bi-modal) in a desert generally is similar across large areas (Beatley, 1974a; Went, 1949); therefore, data we used were appropriate for a general characterization of our study sites. Indeed, moisture content of forage generally followed patterns of precipitation on our study areas, with shrubs at Old Dad Peak possessing the highest moisture content across seasons, and perennial forbs and perennial grasses also responding to autumnal rainfall on that study site (Table 2.3).

Female mountain sheep from the Panamint Range and Old Dad Peak used different life-history strategies to cope with these disparate environments. Perhaps most notable were differences of home-range size between areas (Table 2.1); our findings supported the hypothesis that females from the Panamint Range would have larger home ranges than conspecifics from Old Dad Peak. That result (Table 2.1) also supported the hypothesis of McNab (1963), even for two populations of the same species in close geographic proximity.

Composition of diets differed markedly for populations of desert sheep inhabiting our two study areas (Table 2.4); females from the Panamint Range foraged predominantly on shrubs, whereas those from Old Dad Peak foraged primarily on forbs and grasses. Welles and Welles (1961) attributed the reliance of mountain sheep on shrubs to the ability of those plants to resist excessive aridity and heat throughout the seasons, and to the general scarcity of grasses and forbs resulting from infrequent precipitation. That forbs and grasses should be scarce in the Panamint Range was further supported by Beatley (1974*b*), who reported that changes in plant phenology in the Mojave Desert were triggered by rainfall events >25 mm, which brought soil moisture to field capacity. Beatley (1974*b*) noted that adequate precipitation occurring between late September and early December was the precursor to vegetative growth and successful reproduction among shrubs the following spring, and was essential for growth and reproduction of herbaceous perennials and annuals the following spring. Long-term data (1948-1989) from near the Panamint Range revealed that only 25% of 42 years received sufficient precipitation (>25 mm) in any month between September and December to initiate plant growth. Because those data were available only as monthly, rather than daily totals, they did not represent individual precipitation events, and 25% probably overestimates years when adequate precipitation would have existed. Indeed, only one precipitation event >25 mm occurred during 1995-1997 when rainfall was tallied daily. Thus, adequate precipitation occurred neither for vegetative growth nor for reproduction of annuals or herbaceous perennials.

In contrast, long-term data for Old Dad Peak (Fig. 2.1*a*) indicated that precipitation in 33% of 42 years would have been adequate for growth and reproduction of most plants. Furthermore, data from a site nearer Old Dad Peak (Baker, CA) revealed

that during 1983-1989, 3 of 7 years received >25 mm of precipitation during September-December. Mountain sheep near Old Dad Peak would be more likely than those in the Panamint Range to experience a year when plants received enough precipitation during the critical period for growth and reproduction.

Our prediction that forage would be of higher quality and more abundant at Old Dad Peak than in the Panamint Range was supported (Table 2.3, Fig. 2.4). Female mountain sheep from Old Dad Peak responded to growth and abundance of forbs in spring by increasing their use (49%) of that forage (Table 2.4). Coincident with the highest use of forbs by females at Old Dad Peak during spring were highest values of FN, followed by a gradual decline in that measure, with autumn being lowest (Fig. 2.5). That same pattern was evident for measures of forage quality (Table 2.3); thus, FN was a reasonable indicator of general range condition for our study areas, as reported for other locations by Hodgeman and Bowyer (1986), Rachlow and Bowyer (1994) and Nicholson et al. (in review).

Proportion of forage classes in diets of female mountain sheep from the Panamint Range remained similar across seasons, and shrubs were most prevalent (Table 2.4). Indeed, our results also supported the notion that reliance on shrubs by sheep from the Panamint Range would be the best strategy to ensure a consistent source of nutrients.

Warrick and Krausman (1989) suggested that succulents were an important component in the diets of desert mountain sheep. Mountain sheep from the Panamint Range used succulents (i.e., cacti) more than did females from Old Dad Peak (Table 2.4), but proportion of succulents in diets of sheep from the Panamint Range remained constant among seasons (Table 2.4). This result emphasized that succulents were a critical component of the diets throughout the year in that extremely dry and hot

environment. Because succulents are low in protein ($< 5\%$; Seegmiller et al., 1990), use of that resource likely reflected the need to maintain water balance. We hypothesize that consumption of succulents by female mountain sheep in the Panamint Range reduced their dependence on free water, and thereby increased the area over which they could forage in that depauperate environment. Indeed, mountain sheep from the Panamint Range were farther from water during all seasons than were females from Old Dad Peak (Table 2.2). The amount and timing of precipitation near Old Dad Peak were more favorable than in the Panamint Range for the production of forage (Beatley, 1974*b*). Hence, mountain sheep at Old Dad Peak likely had to search a smaller area for nutritious forage, with a higher moisture content than in the Panamint Range and, consequently, exhibited smaller home ranges.

We rejected our prediction that quality of diets (FN) would be higher for females at Old Dad Peak than for those in the Panamint Range (Fig. 2.5). Quality of forage generally was higher at Old Dad Peak, but seasonal variation occurred for forage classes (Table 2.3). One potential explanation for differences between study sites in FN during summer and autumn was that protein-binding phenolics (e.g., tannins) may have elevated FN (Robbins et al., 1987) for females from the Panamint Range (Fig. 2.5). Because phenolics can be associated with browse species (Van Soest, 1994), increased FN for females from the Panamint Range during summer and autumn may have been associated with their increased consumption of shrubs. Because there was no association between the shrub component in diets and FN in either study area, phenolics probably did not confound our analyses of FN markedly. An alternative explanation was that both populations of mountain sheep were near the ecological carrying capacity (K) of their environments as evidenced by similar young:adult female ratios and similar body size

when corrected for age. Nicholson et al. (in review) demonstrated that increased population size relative to K could lower values for FN.

The absence of differences in mean body size of female sheep from the Panamint Range and those near Old Dad Peak indicated that differences in sizes of home range between those areas were not likely a consequence of differences in metabolic requirements (Swihart et al., 1988). Moreover, no apparent relationship existed between size of home range and ages of females from either the Panamint Range or Old Dad Peak (Fig. 2.3). Our analysis of size of home range and body size for female mountain sheep in the Panamint Range failed to demonstrate a meaningful relation between those variables. Social structure of female sheep, which included maternal groups, reduced the probability of females of different ages exhibiting dissimilar home-range sizes. Thus, differences in size of home range reflected ecological relationships between mountain sheep and their environments.

Population density was nearly four-fold higher at Old Dad Peak than in the Panamint Range, although we believe both populations were near K . Difference in the densities of mountain sheep, however, was not likely the reason underpinning the disparity in size of home ranges. Mountain sheep are not territorial (Bowyer and Leslie, 1992; Shackleton, 1985); indeed, we observed substantial overlap in the home ranges of females on both our study sites. If higher density alone increased size of home ranges via intensified scramble competition, then a pattern opposite the one we observed should have occurred.

Krausman et al. (1989) compared mean home-range size between two subpopulations of mountain sheep occupying adjacent areas. Home ranges were larger where resources were more limited, and greater diversity of plant species and more forage

occurred where home ranges were smallest (Krausman et al., 1989). Those authors concluded that sizes of home ranges were related to factors other than climate: most notably habitat quality and, to a lesser extent, age, social status, and the presence of interspecific competitors. We concur with Krausman et al. (1989) that habitat quality is the most important factor determining size of home range for desert mountain sheep, and was likely responsible for most of the differences we observed. Nonetheless, our data also demonstrated that patterns of precipitation in the Panamint Range and at Old Dad Peak played a critical role in affecting plant productivity and abundance, and thereby influenced home-range size of mountain sheep. Clearly, those desert populations of mountain sheep employed differential home-range strategies to cope with the inhospitable and highly variable environments in which they occurred.

Our results indicated critical links among amount and pattern of precipitation, production of forage, and population characteristics of mountain sheep in variable environments, including diet, home-range size, and population density. Clearly, population size and variability are important components in the persistence of these unique ungulates in desert ecosystems (Bleich et al., 1996; Krausman 1997; Schwartz et al., 1986). Considerable differences of opinion exist over the role of precipitation in the persistence of populations of mountain sheep (Berger, 1990, 1999; Wehausen, 1999). We believe, however, that both the amount and timing of precipitation, and the relative relationships of populations to K (Douglas and Leslie, 1986), must be considered to resolve this important issue. Further research on how these critical factors interact to affect the viability of mountain sheep in desert environments clearly is warranted.

ACKNOWLEDGMENTS

We thank A. Pauli, T. Swank, C. Baker, W. Allsup, D. Racine, J. Schlachter, K.

Pindel, D. Threlhoff, and K. Whitten for field assistance, L. Oehler and M. Oehler, Jr. for assistance with forage samples, S. DeJesus for piloting the helicopter, R. Teagle, B. Nuckolls, B. Gonzales, M. Chechowitz, and others at the California Department of Fish and Game Wildlife Investigations Laboratory for assistance with captures, and R. Anthes, T. Evans, and E. Forner for flying aerial-telemetry surveys. We are especially grateful to S. Torres for his assistance. This study was supported indirectly by Canyon Resources Corporation, through the Institute of Arctic Biology at the University of Alaska Fairbanks, California Department of Fish and Game, North Dakota Game and Fish Department, United States Bureau of Land Management, United States National Park Service, and the San Fernando Valley Chapter of Safari Club International. We thank J. Sedinger for helpful comments on the manuscript. This is a contribution from the California Department of Fish and Game Mountain Sheep Conservation Program, and is Professional Paper 017 from the Eastern Sierra Center for Applied Population Ecology.

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Table 2.1.—Size of adaptive kernel (ADK) and minimum convex polygon (MCP) home ranges (ha) and CV (%) for female mountain sheep from Old Dad Peak (n = 15), San Bernardino Co., California, (1986-1989), and the Panamint Range (n = 15), Inyo Co., California, (1995-1997). P-values from t-tests are for within-row comparisons (Old Dad Peak versus Panamint Range).

		Area						
		Old Dad Peak			Panamint Range			
Home-range								
model		\bar{X}	SD	CV	\bar{X}	SD	CV	P -value
ADK								
95%		3,448	2,059	60	6,598	2,205	33	≤ 0.001
50%		514	344	67	1,101	459	42	≤ 0.001
MCP ^a								
95%		2,269	1,242	55	3,754	1,157	31	≤ 0.001

^aMinimum convex polygon home range presented for comparison with other studies.

Table 2.2.—Mean difference (m) between the distance that radiocollared female mountain sheep and an equal number of random locations occurred from sources of permanent water at Old Dad Peak, San Bernardino Co., California, (1986-1989), and the Panamint Range, Inyo Co., California, (1995-1997). P-values are from one-way ANOVAs (area as main effect) conducted by season for within-row comparisons (Old Dad Peak versus Panamint Range).

Season	Study area						<i>P</i> -value
	Old Dad Peak			Panamint Range			
	\bar{X}	<i>SD</i>	<i>n</i>	\bar{X}	<i>SD</i>	<i>n</i>	
Spring	-2,838 ^a	3,511	192	-704	1,387	118	0.001
Summer	-2,971	2,935	250	-821	1,204	274	0.001
Autumn	-1,538	3,265	241	-721	1,253	184	0.001

^aMinimum convex polygon home range presented for comparison with other studies.

Table 2.3.—Mean percent crude protein, in vitro dry matter digestibility (IVDMD), and moisture of selected perennial forbs, perennial grasses, and shrubs from locations near Old Dad Peak, San Bernardino Co., California, (1990-1991), and the Panamint Range, Inyo Co., California (1995-1996). P-values for within-row (Old Dad Peak versus Panamint Range) comparisons are from one-way ANOVAs with a Bonferroni correction for multiple comparisons.

Season and forage	Study area						<i>P</i> -value
	Old Dad Peak			Panamint Range			
	\bar{X}	<i>SD</i>	<i>n</i> ^a	\bar{X}	<i>SD</i>	<i>n</i>	
Spring							
Protein (%)							
Forbs	15.5	2.9	8	12.0	7.0	22	ns ^b
Grass	6.3	3.2	32	5.8	0.9	6	ns
Shrubs	10.4	4.8	76	10.8	6.1	56	ns
IVDMD (%)							
Forbs	53.5	9.3	8	34.3	11.5	22	≤ 0.05
Grass	37.1	7.1	32	54.3	13.8	6	≤ 0.05
Shrubs	42.3	16.5	76	52.1	16.2	56	≤ 0.05
Moisture (%)							
Forbs	36.7	28.2	71	25.2	24.0	55	ns
Grass	28.5	17.4	130	21.5	10.8	40	ns
Shrubs	44.6	16.5	139	38.8	18.8	310	≤ 0.05
Summer							
Protein (%)							
Forbs	15.8	2.8	22	9.8	2.9	8	≤ 0.001
Grass	8.1	2.8	36	4.3	1.1	6	≤ 0.05

Shrubs	11.0	4.6	42	9.2	4.5	81	ns
IVDMD (%)							
Forbs	55.8	5.9	22	36.0	16.2	8	≤ 0.05
Grass	41.1	6.5	36	52.1	12.4	6	≤ 0.05
Shrub	44.4	16.4	42	47.0	16.4	81	ns
Moisture (%)							
Forbs	37.2	18.7	76	33.0	15.7	55	ns
Grass	33.7	18.5	135	12.2	6.9	39	≤ 0.001
Shrubs	43.0	14.7	114	32.1	12.7	307	≤ 0.001
Autumn							
Protein (%)							
Forbs	11.4	2.7	14	11.6	7.5	8	ns
Grass	6.1	1.8	36	3.8	0.5	12	≤ 0.01
Shrubs	9.4	3.1	80	9.6	5.3	36	ns
IVDMD (%)							
Forbs	48.1	3.3	14	40.5	16.7	8	ns
Grass	42.3	6.04	36	44.3	5.3	12	ns
Shrubs	43.5	15.1	80	50.2	16.9	36	ns
Moisture (%)							
Forbs	39.6	11.2	70	32.2	20.3	43	ns
Grass	16.5	12.8	155	8.06	5.32	53	≤ 0.001
Srubs	37.9	14.3	110	28.6	19.1	229	≤ 0.001

^ans = not significant after Bonferroni correction ($P > 0.05$)

Table 2.4.—Percent of forbs, grasses, shrubs, and succulents (mostly cacti) in the diets of female mountain sheep, indexed from microhistological analyses of their feces, from locations near Old Dad Peak ($n = 122$ fecal groups), San Bernardino Co., California, (1990-1991), and the Panamint Range ($n = 25$ composite groups), Inyo Co., California, (1995-1996). P-values for within-row comparisons from one-way ANOVAs with a Bonferroni correction for multiple comparisons.

Season	Study area				<i>P</i> -value
	Old Dad Peak		Panamint Range		
	\bar{X}	<i>SD</i>	\bar{X}	<i>SD</i>	
Forage class					
Spring					
Forbs	49.2	14.2	32.7	9.0	ns ^a
Grasses	28.0	15.9	1.7	2.4	0.001
Shrubs	22.0	14.8	54.6	13.6	0.001
Succulents	0.3	0.6	11.0	6.4	0.001
Summer					
Forbs	36.3	14.7	27.3	11.5	ns
Grasses	35.8	16.5	3.7	3.0	0.001
Shrubs	26.2	19.8	57.8	12.2	0.001
Succulents	1.8	3.2	11.2	4.3	0.001
Autumn					
Forbs	28.8	17.6	35.2	7.8	ns
Grasses	40.8	26.6	6.2	2.4	0.05
Shrubs	28.4	27.5	48.9	7.8	ns
Succulents	2.1	4.8	9.7	5.6	0.01

^ans = not significant after Bonferroni correction ($P > 0.05$)

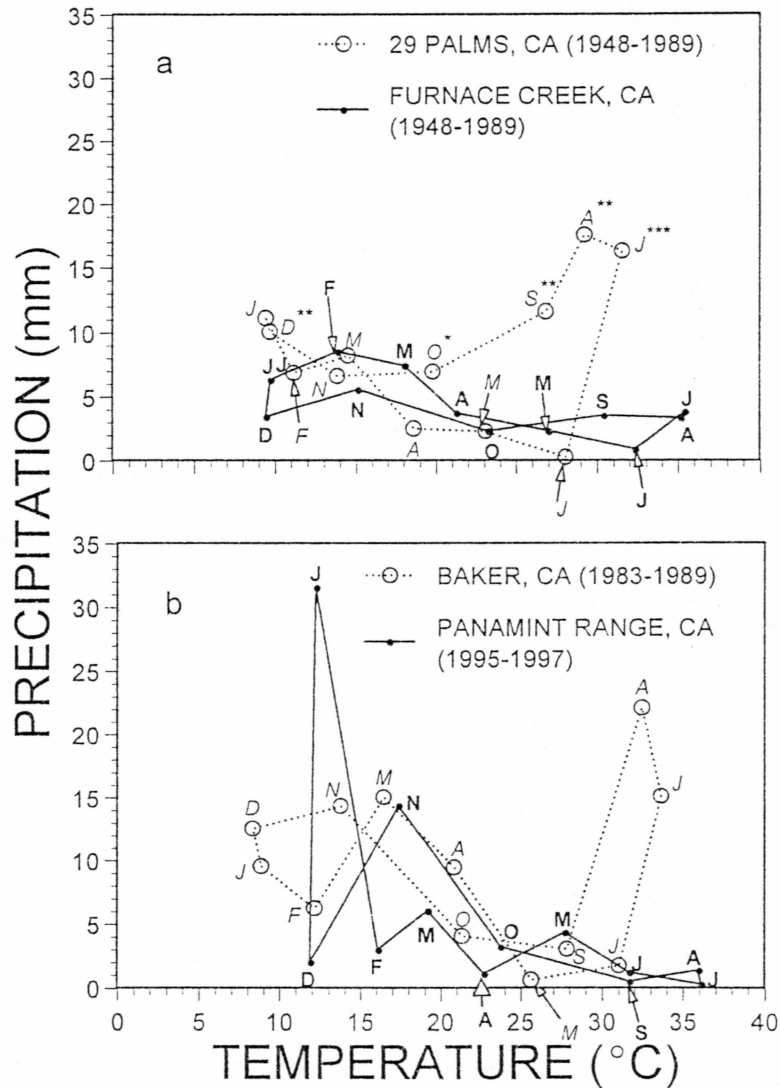


Fig. 2.1.--Climographs of mean monthly temperature and precipitation at Twentynine Palms, San Bernardino County, California, (1948-1989), Furnace Creek-Greenland Ranch, Inyo County, California, (1948-1989), Baker, San Bernadino County, California, (1983-1989), and the Panamint Range, Inyo County, California, (1995-1997). Asterix adjacent to months (letters) indicate that area had significantly greater mean precipitation (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

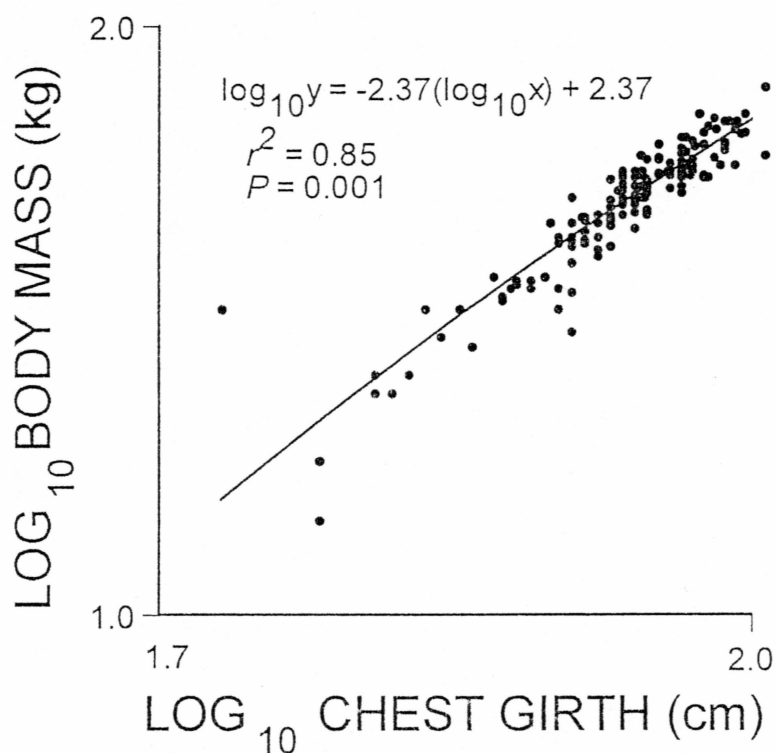


Fig. 2.2.--Relationship between \log_{10} chest girth and \log_{10} body mass for 155 female mountain sheep captured near Old Dad Peak, San Bernardino County, California, (1983-1989).

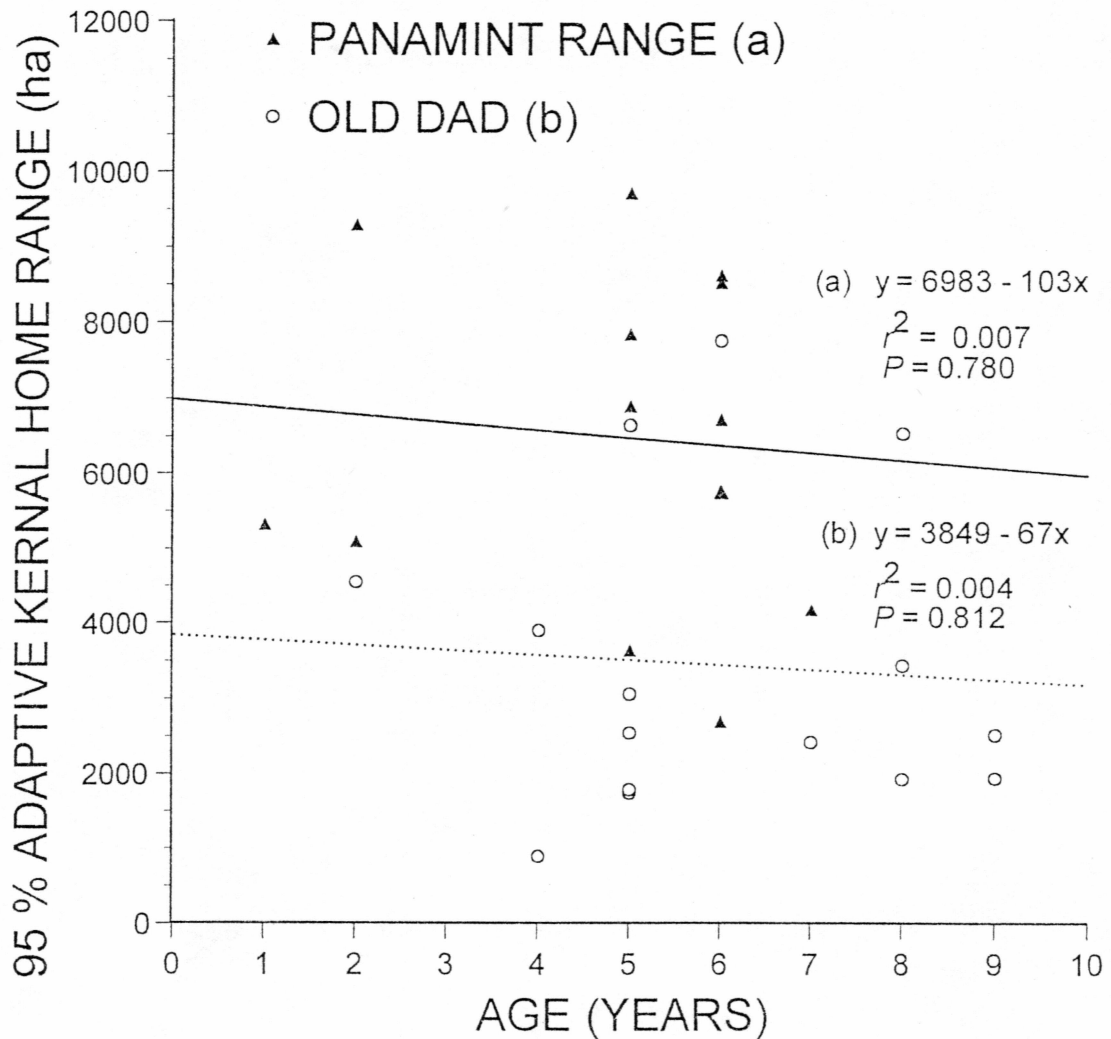


Fig. 2.3.--Relationship between age and size of 95% adaptive kernel home range for radiocollared female mountain sheep from the Panamint Range, Inyo County, California, ($n = 13$; 1995-1997), and near Old Dad Peak, San Bernardino County, California, ($n = 15$; 1986-1989).

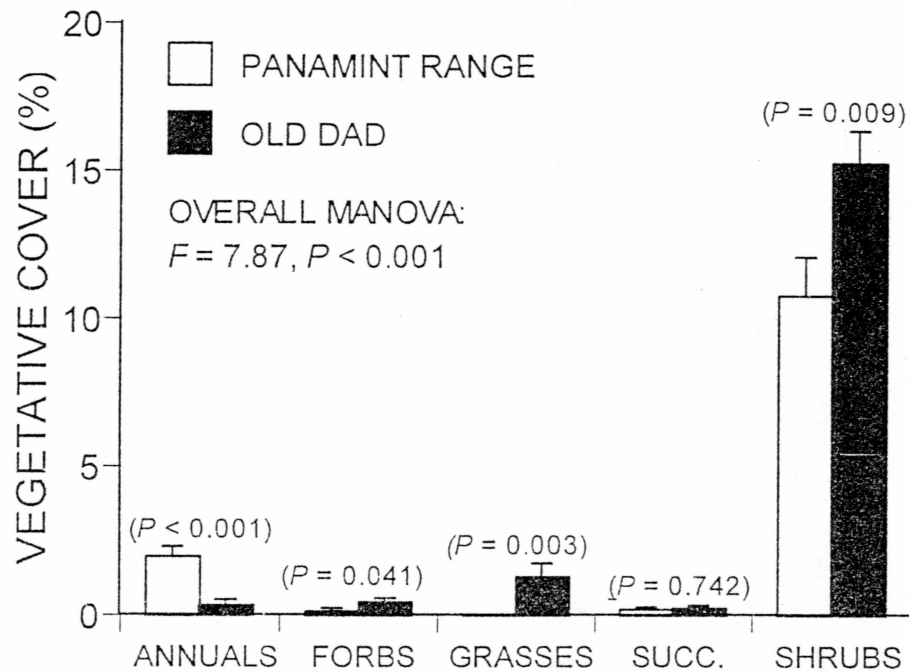


Fig. 2.4.--Mean ($\pm SE$) vegetative cover (%) in habitats used by radiocollared female mountain sheep from the Panamint Range, Inyo County, California ($n = 18$ transects), and near Old Dad Peak, San Bernardino County, California ($n = 19$ transects). Percent bare ground was significantly greater ($P = 0.010$) in Panamint Range (87%) than at Old Dad Peak (82%).

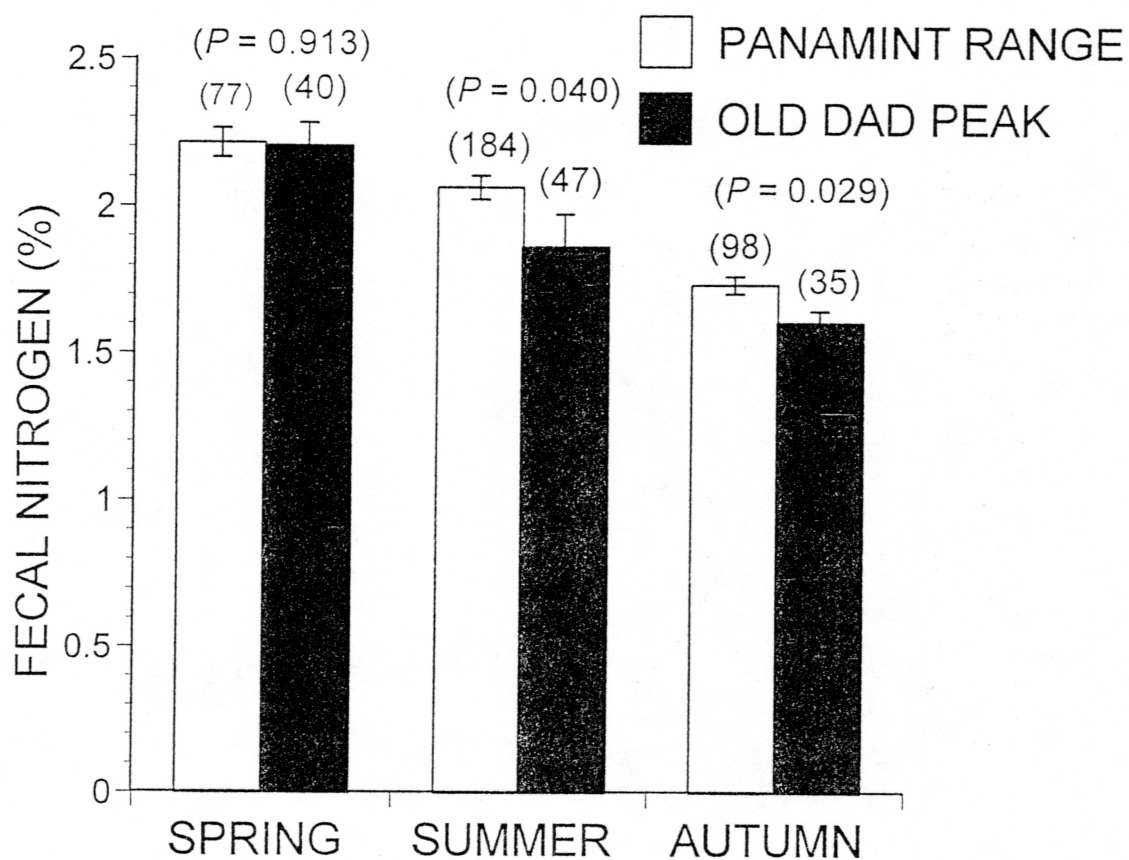


Fig. 2.5.--Mean (+ SE) fecal nitrogen (%) of mountain sheep inhabiting female ranges from the Panamint Range, Inyo County, California, (1995-1997), and near Old Dad Peak, San Bernardino County, California, (1987-1990). Numbers above bars represent sample size.